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9620 Heather Road
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TEL (310) 399 6016
E-MAIL: Editorial: mattoni@ucla.edu
Business: mattoni@ucla.edu
Technical: jrl_lepidoptera@yahoo.com

FOUNDER: William Hovanitz (1915-1977)

EDITORIAL STAFF: Andrew Warren, editor E-MAIL: jrleditor@yahoo.com
Rudolf H.T. Mattoni, assistant editor E-MAIL: mattoni@ucla.edu
Nancy R. Vannucci, managing editor E-MAIL: jrl_lepidoptera@yahoo.com

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MANAGING EDITOR AT THE ADDRESS: Nancy R. Vannucci, Maza 3340, Morón B1708GOP, Buenos Aires, Argentina

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Total sperm ejaculation in monandrous (*Papilio machaon*) and polyandrous (*P. xuthus*) swallowtail butterflies (Lepidoptera: Papilionidae) restricted to larval stage-derived nutrients

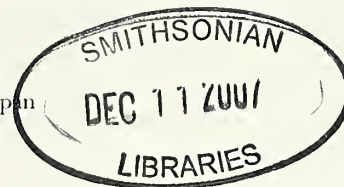
MAMORU WATANABE

Institute of Biological Sciences, University of Tsukuba, Tsukuba, Ibaraki 305-8572, Japan

E-mail: watanabe@kankyo.envr.tsukuba.ac.jp

TAIHEI KOBAYASHI

Institute of Biological Sciences, University of Tsukuba, Tsukuba, Ibaraki 305-8572, Japan



Abstract: Potential capacities of male swallowtail butterflies for ejaculation containing sperm were examined in laboratory studies in monandrous (*Papilio machaon*) and polyandrous (*P. xuthus*) species. Virgin males transferred a spermatophore and accessory substances that corresponded to an average of 2.4% and 2.1% of their body weight at eclosion in *P. xuthus* and *P. machaon*, respectively. The spermatophore contained about 41 and 120 eupyrene sperm bundles and 247,000 and 202,000 apyrene spermatozoa for *P. xuthus* and *P. machaon*, respectively. Individual eupyrene and apyrene spermatozoa of *P. machaon* were smaller than those of *P. xuthus*. However, when the males re mated at two days after the first mating, they produced a spermatophore of 55% and 32% of full size in *P. xuthus* and *P. machaon*, respectively. The number of eupyrene sperm bundles in the second spermatophore increased while the apyrene spermatozoa decreased in *P. xuthus*. The larger number of eupyrene sperm bundles and the relatively smaller number of apyrene spermatozoa in the first and the second mating of *P. machaon* compared to *P. xuthus* are discussed from the viewpoint of female monandry and polyandry.

Key words: apyrene sperm, eupyrene sperm bundle, *Papilio machaon*, *Papilio xuthus*, second mating, spermatophore.

INTRODUCTION

In many butterfly species, the male's second spermatophore is significantly smaller than his first (Svärd & Wiklund 1986, 1989; Oberhauser 1988). Before production of a second spermatophore of full size, a resting period of several days is required, during which the male's activity consists of feeding, flying, avoiding predators, and so on (Watanabe & Hirota 1999). The copula duration of the second mating is often significantly longer than that of the first, probably due to the size of the ejaculate (Svärd & Wiklund 1986; Kaitala & Wiklund 1995).

Among the yellow swallowtail butterflies in Japan, females of *Papilio xuthus* Linne (Papilionidae) mate three times during their life span while females of *P. machaon hippocrates* C. et R. Felder are apt to be monandrous (Watanabe & Nozato 1986). For polyandrous species like *P. xuthus*, each mating provides the female with nutrients and some alkaloids with both transferred to her via the male's spermatophore (LaMunyon & Eisner 1994). It has been suggested that

butterfly females can use such male-derived nutrients for somatic maintenance, to enhancement of their fecundity, and to increase fitness of their offspring (Friedel & Gillott 1977; Watanabe 1988; Boggs 1990). The potential importance of male-derived nutrients might correlate positively with the size of the male ejaculate and the degree of female polyandry (Svärd & Wiklund 1989). When the male re mates, he must produce another spermatophore of sufficient size with a sufficient number of sperm in order to fertilize as many eggs as possible. Therefore, the duration of the male's recovery time and the rate of recovery in terms of spermatophore size and sperm number are important for males under sperm competition (Watanabe & Hirota 1999; Wedell & Cook 1999a). The former correlates with the duration of the female's non-receptive refractory period following mating (Kaitala & Wiklund 1995), and high sperm numbers seemed to be advantageous in sperm competition (Parker 1992). Rather than utilizing the sperm of all her mates, the female uses predominantly those from the last partner in *P. dardanus* (Simmons & Siva-Jothy 1998). On the other hand, for monandrous species like *P. machaon*, the female may not exercise such postcopulatory sperm selection (Sims 1979). Intact

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spermatophores have been observed in the bursa copulatrix of aged females of monandrous species, such as *P. machaon* (unpublished) and *Lycaena phlaeas* (Watanabe & Nishimura 2001), suggesting that these females did not use male ejaculate to obtain the nutrients necessary for reproductive success.

Most butterfly species produce two types of sperm, eupyrene and apyrene, which can often represent up to 90% of the total sperm number (Cook & Wedell 1996; Watanabe et al. 1998a, b). Males vary the size of spermatophores produced as well as the number of both types of sperm transferred depending on their mating status (Cook & Wedell 1996; Wedell & Cook 1999b). Previously mated males of *P. xuthus* produce spermatophores that are about half the size of those they produced as virgins, when they used nutrients derived only from their larval stages (Watanabe & Hirota 1999). However, there have been no studies on sperm competition in swallowtail butterflies. The aim of this study was to compare male's exploitation of larval stage-derived nutrients for spermatophore production between monandrous and polyandrous swallowtail butterfly species in terms of copula duration, spermatophore mass, and the number of apyrene and eupyrene spermatozoa produced.

MATERIALS AND METHODS

General methods

One and three-day-old males were mated with virgin females of both *P. xuthus* and *P. machaon*. Sperm transfer from the males to spermatophore was assessed immediately after copulation. All animals were obtained from a continuously breeding culture reared in the laboratory at room temperature in the summers of 2001 and 2003. Adults were collected in the field, and females were allowed to oviposit on leaves of *Citrus unshu* (Rutaceae) for *P. xuthus* and those of *Heracleum lanatum* (Umbelliferae) for *P. machaon*. Larvae of both species were reared in the laboratory under an 18-h light 6-h dark regime at 25°C to avoid diapause. All the pupae were placed in an emergence cage to ensure normal eclosion. Adults were weighed on the day of eclosion and given a unique mark on the hind wing with a felt tipped pen. Then, males were maintained in flight cages (30×40×45 cm) without intake of any nutrients; i.e., they were fed on only water during their life span. On the other hand, females were kept in individual envelopes (14L10D light cycle at a temperature of 26–27°C) to maintain their virginity. The mean weight of male at emergence was 453.5±63.6 mg for *P. xuthus* and 588.1±128.3 mg for *P. machaon* (±SD). One of the best indicators of nutrients obtained dur-

ing the larval stage is butterfly mass.

Because the mating ability of males on the day of eclosion is low, we hand-paired one-day old males with virgin females (one to three-days old) in the morning. Hand-pairing is widely used in the laboratory rearing of butterflies (West 1983; Scriber & Lederhouse 1988; Watanabe & Hirota 1999). In this study, we brought the tips of the male and female abdomens together, squeezed the male in order to open his claspers, and then joined him with the female. After joining, the pair was removed to a small cage and the copula duration was recorded.

Males were returned to the flight cages immediately after their first mating and held to attempt a second copulation three-days-later with virgin females. A total of 26 mated males for *P. xuthus* and 24 mated males for *P. machaon* were hand-paired. Spermatophore mass and the number of eupyrene sperm bundles and apyrene spermatozoa in the spermatophore were determined. Because the accessory substances were ejaculated outside the spermatophore into the bursa copulatrix of the female, we could easily separate them during the dissection of the bursa copulatrix.

Immediately after copulation, the females were decapitated and dissected under a stereo microscope to measure the weight of ejaculates in the bursa copulatrix. The intact spermatophore and gel-like accessory substances were weighed (accuracy, 0.001 mg). Males that had successfully mated twice were returned to flight cage to attempt a third copulation.

Sperm counting procedure

The procedure used for sperm counting has been described in detail in Watanabe et al. (1998a, b). We evaluated the number of both types of sperm derived in females by counting the number of sperm in the transferred spermatophore. Immediately after copulation, the eupyrene sperm are packed in the spermatophore in a bundle, whereas the apyrene bundle has already dissolved, and thus the apyrene sperm can be observed individually (Katsuno 1977). Eupyrene sperm bundles are clearly visible at ×40 magnification and apparently uniform in size. Therefore, we first mechanically disrupted the spermatophore and directly counted the eupyrene sperm as a bundle using a stereo microscope. Then, all of the ejaculate was washed out into a small tube containing a known volume of saline solution (Ringer's solution for insects). The tube was gently stirred for 1 min in order to homogenize the sperm suspension. A total of six, 10 µl subsamples were removed from each sample using a Gilson autopipette and allowed to dry on slides under dust covers. The dry slides were then dipped

for about 3 sec in distilled water and again allowed to dry. Each subsample was examined under a darkfield phasecontrast microscope ($\times 100$) to count the numbers of apyrene sperm and eupyrene single sperm.

The total number of apyrene spermatozoa in a spermatophore was calculated by multiplying the average sperm count in 10 μ l of suspension by its dilution factor. All means are shown with their standard errors. All weights were determined to the nearest 0.001 mg.

RESULTS

All one-day-old (one day after eclosion) virgin males of both species were successfully mated to females by the hand-pairing. Each mean duration for copulation of the first mating was about one hour, without a significant difference between the species (Table 1). Although several mated males of both species failed to copulate in the second mating, the copula duration of successfully re mated males was also about one hour, which was not significantly different from that of the first matings. The reasons for failure included inability to conjoin or failure to transfer a spermatophore after long in copula duration. No males successfully mated a third time. There was no relation between copula duration and the spermatophore weight in virgin males. Table 2 shows that a virgin male of *P. xuthus* transferred a spermatophore of about 5.5 mg with accessory substances of about 5.2 mg to the female bursa copulatrix. Therefore, virgin males produced ejaculates of 10.7 mg, or 2.4% of their body weight at eclosion. Mated males then produced a subsequent spermatophore of 3.0 mg with accessory substances of 2.9 mg, both of which weights were 55% of those from the first mating.

For *P. machaon*, on the other hand, a virgin male transferred a spermatophore of about 8.0 mg with accessory substances of about 4.1 mg to the female bursa copulatrix, and both of these weights were sig-

nificantly different from those of *P. xuthus* (Table 2). Therefore, virgin males produced ejaculates of 12.1 mg, or 2.1% of the body weight at eclosion. Mated males then produced a subsequent spermatophore of 2.6 mg, which was not significantly different from that of mated males of *P. xuthus*. This value was 32% of the spermatophore size of the first mating. The mass of accessory substances (1.3 mg) from the mated males was also 33% of that from the virgin males.

There was no relationship between the spermatophore weight and the copula duration in the mated males ($F=0.971$ in *P. xuthus* and $F=0.333$ in *P. machaon*). Since the copula duration at each mating for each species was roughly one hour, the ejaculation speed was a function of the mass when the copulation terminated. Therefore, the speed at the first mating was higher than that at the second mating, and the difference of the speed between the first and the second mating in *P. machaon* was longer than that in *P. xuthus*. In addition, spermatophore weight of the mated males depended on that of the first mating in *P. xuthus* ($F=10.365$, $P<0.01$). Males that produced a larger spermatophore at the first mating also produced a larger one at the next mating, though the mass of the second spermatophore was generally half that of the first mating. By contrast there was no trend in regard to spermatophore mass between the first and the second mating in *P. machaon* ($F=0.333$).

All spermatophores in this study included both eupyrene sperm bundles and apyrene sperm. Since the bundles were usually coming loose and meandering widely under the microscope, we measured the length of a free eupyrene spermatozoon instead of the bundle. For *P. xuthus*, the length of a eupyrene spermatozoon was 916.7 ± 44.0 μ m (10 males), and that of an apyrene spermatozoon was 627.9 ± 8.3 μ m. For *P. machaon* (10 males), the length of a eupyrene spermatozoon was 562.5 ± 11.0 μ m, and that of an apyrene one was 274.5 ± 10.5 μ m. Therefore, both eupyrene and apyrene spermatozoa of *P. machaon* were smaller than those of *P. xuthus* ($U=0.00$, $P<0.01$ and $U=0.00$,

Table 1. Copula duration for *P. xuthus* and *P. machaon* males that were successful at the first and the second mating (min, \pm SE, Mann-Whitney U-test).

	1st mating	2nd mating	
<i>P. xuthus</i>	59.3 \pm 4.5 (n=15)	62.6 \pm 3.4 (n=15)	U=91.5, n.s.
<i>P. machaon</i>	55.3 \pm 2.7 (n=13)	56.3 \pm 3.3 (n=15)	U=92.5, n.s.
	U=87.0, n.s.	U=79.0, n.s.	

n: number of males

Table 2. Ejaculate mass transferred from *P. xuthus* and *P. machaon* males that were successful at the first and the second mating (mg, \pm SE, Mann-Whitney U-test).

		1st mating	2nd mating	
Spermatophore	<i>P. xuthus</i>	5.50 \pm 0.25 ^a (n=15)	3.03 \pm 0.20 ^b (n=15)	U= 5.0, P<0.01
	<i>P. machaon</i>	8.03 \pm 0.35 ^a (n=13)	2.60 \pm 0.19 ^b (n=16)	U= 0.0, P<0.01
Accessory substances	<i>P. xuthus</i>	5.17 \pm 0.26 ^c (n=15)	2.89 \pm 0.16 ^d (n=15)	U= 6.0, P<0.01
	<i>P. machaon</i>	4.05 \pm 0.55 ^c (n=13)	1.33 \pm 0.22 ^d (n=16)	U=11.0, P<0.01

n: number of males

a: U=9.5, P<0.01

b: U=90.0, n.s.

c: U=47.0, 0.05>P>0.01

d: U=17.5, P<0.01

P<0.01, respectively).

Table 3 shows that virgin males of *P. xuthus* transferred about 41 eupyrene sperm bundles in one spermatophore. There was no relation between the number of bundles and the spermatophore weight for the first mating (F=0.025), e.g. the number of eupyrene sperm bundles did relate to spermatophore size. In fact, the mated males transferred about 60 eupyrene sperm bundles, which was significantly larger than the number at the previous mating, though the spermatophore weight at the second mating was significantly lighter. There was no significant relation between the number of bundles and the spermatophore weight at the second mating (F=0.243).

For *P. machaon*, on the other hand, a virgin male transferred about 120 eupyrene sperm bundles in a spermatophore, and there was a positive correlation between spermatophore weight and the number of bundles (F=8.690, 0.05>P>0.01), ranging 71 to 192 bundles and 6.2 to 9.8 mg in weight. A virgin male transferred about three times the number of bundles in *P. xuthus* (Table 3). Then, the mated males of *P. machaon* produced about 134 bundles, which was not significantly different from the number of bundles at the previous mating. There was no significant relation between the number of bundles and the spermatophore weight at the second mating (F=0.787).

There was no relation between the number of apyrene spermatozoa and the spermatophore weight for either the first (F=0.007) or the second (F=0.534) matings in *P. xuthus*. The number of apyrene spermatozoa at the first mating was significantly larger than that at the second mating, suggesting that at the second mating males transferred more eupyrene and

less apyrene spermatozoa irrespective of their second mating ejaculate mass, but related to mating status.

There was no relation between the number of apyrene spermatozoa and the spermatophore weight for either the first (F=1.212) or the second (F=0.373) matings in *P. machaon*. The number of apyrene spermatozoa at the first mating was significantly smaller than that in *P. xuthus*, but not significantly larger than that at the second mating.

DISCUSSION

Although copula duration in butterflies seems to be under male control (Wickman 1985), one of the possible costs of mating incurred by males in transferring spermatophores is time. Many butterflies try to decrease copula duration against the risk of predation (Rutowski 1984), while prolonged mating has a function other than just spermatophore transfer irrespective of the size. In pierid butterflies differential transfer rates are due to behavioral competition among males (Sv rd & Wiklund 1988; Watanabe et al. 1997). In this study, however, copula duration of the second mating with small spermatophores in both *P. xuthus* and *P. machaon* was not longer than the first, unlike in other butterfly species (Sv rd & Wiklund 1986; Kaitala & Wiklund 1995).

Male *P. xuthus* produce full-size spermatophores when virgins, or when they mate after several days of abstinence (Watanabe & Hirota 1999). The present study shows that, during an abstinence period, mated males produce a spermatophore that is 55% (*P. xuthus*) and 33% (*P. machaon*) of the size of a full-size spermatophore. In many butterfly species, the second

Table 3. Number of eupyrene sperm bundles and estimated number of apyrene spermatozoa in a spermatophore transferred from *P. xuthus* and *P. machaon* males that were successful at the first and the second mating (\pm SE).

		1st mating	2nd mating	
Eupyrene sperm bundles	<i>P. xuthus</i>	41.3 \pm 5.76 ^a (n=14)	59.6 \pm 6.86 ^b (n=14)	U=59.0, P<0.05
	<i>P. machaon</i>	119.8 \pm 13.70 ^a (n=10)	133.7 \pm 14.39 ^b (n=16)	U=72.5, n.s.
Apyrene spermatozoa	<i>P. xuthus</i>	247,435 \pm 30,197 ^c (n=13)	166,100 \pm 20,859 ^d (n=14)	U=52.0, P<0.05
	<i>P. machaon</i>	202,143 \pm 33,719 ^c (n=10)	165,098 \pm 20,888 ^d (n=16)	U=61.0, n.s.

n: number of males

a: U=4.0, P<0.01

b: U=35.0, P<0.01

c: U=39.0, 0.05>P>0.01

d: U=86.0, n.s.

spermatophore is smaller than the first (Sims 1979; Oberhauser 1988; Svård & Wiklund 1989; Watanabe et al. 1998a). Larger spermatophores induce longer periods of sexual unreceptivity in some lepidopteran females (Oberhauser 1989), during which females lay eggs exclusively fertilized by that male. In *Colias eurytheme*, female fecundity has been shown to correlate positively with the size of the received ejaculate (Rutowski et al. 1987). Therefore, a reduction in spermatophore size may potentially be costly in terms of a reduced female reproductive output and shorter female refractory periods. In addition, He & Miyata (1997) have shown that small spermatophores might contain less eupyrene and apyrene spermatozoa than large ones. In the present study, however, the number of eupyrene spermatozoa in the second spermatophore produced by the male was more than that in the first spermatophore for *P. xuthus* and identical to that in the first spermatophore for *P. machaon*. Males of both species were fed only water as adults, meaning that they were using only larval nutrients to produce sperm.

Cook & Wedell (1999) stated that in many butterfly species there are typically 256 eupyrene spermatozoa per bundle. Therefore, the range of approximately 10,000 (=41 \times 256 in *P. xuthus*) to 34,000 (=134 \times 256 in *P. machaon*) eupyrene spermatozoa was above the level guaranteeing adequate fertilization, since a female of either species has fewer than 1000 eggs after eclosion (Watanabe & Nozato 1986). Furthermore, a single eupyrene spermatozoon might be used for insemination of a single egg (Watanabe & Hachisuka 2005). Wedell & Cook (1998) pointed out that mated males compensate by increasing sperm numbers,

resulting in high fertilization success during sperm competition.

For females, the mean lifetime mating frequency is 3 and 1 for *P. xuthus* and *P. machaon*, respectively (Watanabe & Nozato 1986). Svård & Wiklund (1989) also showed that the mean number of mating in the European *P. machaon* was 1.16. Assuming that every female attempted to load a sufficient number of eupyrene spermatozoa for insemination of her eggs, the total number of eupyrene spermatozoa in relation to her fecundity must be similar among species, because the number of eggs in the ovaries was roughly same. A female of *P. xuthus* mated with 3 virgin males during her life span would received 123 (=41 \times 3) eupyrene sperm bundles. This is comparable with the number received at a single mating by a female of *P. machaon*, though the eupyrene spermatozoon size of *P. machaon* was smaller than that of *P. xuthus*. Lastly, a female of *P. xuthus* mating 3 times must receive 750,000 apyrene spermatozoa.

For a male swallowtail butterfly second mating, the probability of encountering non-virgin females who accept copulation must be high in nature, due to the long flying season and to continuous generations during summer. Hence for *P. xuthus*, it may be numbers of eupyrene spermatozoa in spite of reduced nutrient donations. The number of eupyrene sperm bundles in the spermatophore significantly increases for the second mating. During sperm competition, an increased risk with the degree of polyandry, production of high numbers of sperm may be advantageous. In *Pieris rapae*, males transferred significantly more eupyrene sperm on their second mating, although the spermatophore size was reduced (Cook & Wedell

1996; Watanabe et al. 1998a; Wedell & Cook 1999a). Since there might be little sperm mixing in *P. xuthus* due to the apyrene sperm in spermatheca (Watanabe et al. 2000), it appears advantageous for males to transfer an excess of eupyrene spermatozoa with an excess number of apyrene spermatozoa at the second mating.

Male swallowtail butterflies apparently lack means to decrease sperm competition since they leave only a small sperm plug after copulation. Further, males have no provision for removing a rival male's sperm. Their penis cannot reach the spermatheca, where eupyrene sperm is stored. The interval of mating and the morphology of fertilization ducts allow eupyrene spermatozoa from the second mating to be positioned close to the exit. With cul-de-sac spermatheca, the sperm enter and leave by the same duct, such that sperm from the second mating should be the first to leave, resulting in last-male priority in *P. xuthus* (Watanabe et al. 2000). Last-male priority has been established as the predominant pattern of sperm use in most butterfly species that have been studied (Sims 1979, Lederhouse 1981).

On the other hand, females of *P. machaon* seemed not use the spermatophore and accessory substances for either energy or egg production (unpublished) and were monandrous. In fact, they had larger fat bodies in their abdomens after eclosion than *P. xuthus*. This finding corresponds with body weights of the males. Males of *P. machaon* had clearly more fat body than male *P. xuthus*, even though their body sizes were similar. Therefore, non-virgin females of *P. machaon* must have required no further ejaculate from males, and therefore avoided their conspecifics and/or refused mating when males were encountered. Since only virgin females permitted copulation, the operational sex ratio was biased toward males. The probability of mating in males may be low in the field, but the probability of re mating by mated males must be zero if females are able to detect mated males. Then, males of *P. machaon*, particularly virgins, might increase the number of eupyrene spermatozoa as well as the maximum ejaculation mass as much as possible when they copulate. Consequently, sperm size would decrease.

Although the number of apyrene spermatozoa in *P. xuthus* significantly decreased for any second mating, the life time production of apyrene spermatozoa was higher than that in *P. machaon*, particularly in relation to the number of eupyrene spermatozoa. Based on the different amounts of eupyrene and apyrene sperm in the testis (Hiroyoshi & Mitsuhashi 1999), males independently vary the numbers of the two types of sperm ejaculated into the spermatophore (Cook &

Gage 1995; Watanabe et al. 1998b; Wedell & Cook 1999a). The fact that apyrene sperm migrates earlier than eupyrene sperm from spermatophore to spermatheca following copulation suggests that apyrene sperm for the second mating can fill the spermatheca with eupyrene sperm of the first mating in order to prevent fertilization (Watanabe et al. 2000). Therefore, it may be advantageous for *P. xuthus* males to provide polyandrous females with a certain number of large apyrene spermatozoa at each mating to effect sperm competition.

We have no information on the mating frequency of male swallowtail butterflies in nature. We suspect that males of both *P. xuthus* and *P. machaon* mate at intervals of more than a few days, extrapolated in part by their 3-5 weeks life span in the laboratory. Note well that in the present study *P. xuthus* and *P. machaon* males were restricted to larval stage nutrients and never mated more than three times. All males mating only two times died the day after the second mating. Therefore, *P. xuthus* males produced a smaller number of large eupyrene spermatozoa, while *P. machaon* produced a large number of small eupyrene spermatozoa. However, there were more larger apyrene spermatozoa in *P. xuthus* than in *P. machaon*. Consequently, *P. xuthus* males must provide for the extra cost to produce eupyrene sperm and ignore the cost to produce apyrene sperm for each mating under severe sperm competition. By comparison *P. machaon* males decrease the apyrene sperm mass under low sperm competition in the reproductive organs of females. Since survival, and thus mating frequency in nature, should be supported by nutrients from nectar, field studies comparing the mating behavior of *P. xuthus* and *P. machaon* males are necessary.

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Flight Patterns and Mating Behavior in a Zephyrus Hairstreak, *Neozephyrus japonicus* (Lepidoptera: Lycaenidae)

MICHIO IMAFUKU

Department of Zoology, Graduate School of Science, Kyoto University, Sakyo, Kyoto, 606-8502 Japan
ima@ethol.zool.kyoto-u.ac.jp

YASUTOSHI MATSUI¹⁾

Institute for Environmental Management Technology, National Institute of Advanced Industrial Science and Technology, 16-1 Onogawa, Tsukuba, Ibaraki, 305-8569 Japan

HIDEKO MATSUI¹⁾

5-102, 740 Sanuki, Ryugasaki, Ibaraki, 301-0033 Japan

¹⁾ Present address: 7-106, 1-2-63 Fujimi, Higashimurayama, Tokyo, 189-0024 Japan

Abstract: Flight patterns and mating behaviors of a zephyrus hairstreak, *Neozephyrus japonicus*, were investigated in a woodland in Ryugasaki City, Japan, during its adult flight period in late June and July, from 2000 to 2003. This species was most active around dusk, from 17:00 to 18:00 hrs, during which males actively flew around the canopy and edges of the forest. Circling flights performed by two individuals were frequently observed, as were chase flights, sometimes composed of multiple individuals. Circles flown during circling flights averaged 14 cm in diameter and 2.9 rotations/s, thus the velocity of these flights averaged about 130 cm/s. The direction of rotation sometimes changed during circling flights. A third individual occasionally joined a circling flight, which would sometimes disrupt the flight, or rarely, would replace one of the original circlers. Chase flights, sometimes in a zigzag pattern, usually included a female, and sometimes led to the initiation of courtship. Courtship and copulation sometimes occurred just after chase flights. Courtship time was between 30 seconds and one minute, and copulation time varied from 45 minutes to over three hours. Examination of the bursa copulatrix of females of *N. japonicus* from the study site indicated the sporadic occurrence of multiple matings.

Key words: activity time, circling flight, chase flight, mating, Lycaenidae, spermatophore

INTRODUCTION

Butterflies in the tribe Theclini, commonly called "zephyrus hairstreaks" in Japan, are biologically interesting for a variety of reasons. This relatively small group shows great variation in adult and larval morphologies, life histories, physiology, behavior and ecology (Saigusa 1988). In Japan, this group includes 25 species in 13 genera such as *Chrysozephyrus*, *Neozephyrus* and *Favonius*, whose phylogenetic relationships have been studied, using morphological (Shirôzu & Yamamoto 1956) and molecular data (Saigusa & Odagiri 2000).

An intriguing aspect of the Theclini in Japan is variation in wing colors; 13 species show sexual dimorphism, 11 species are nearly or perfectly monomorphic, and 1 species is in an intermediate situa-

tion. Some species of *Chrysozephyrus*, *Neozephyrus* and *Favonius* show the most conspicuous color differences between sexes among butterflies occurring in Japan. These color variations may be related to the behavior and ecology of the various species. Males of some species are territorial, and mate-locate by guarding perches, whereas others mate-locate through patrolling. Adult activity times vary among the different species; some are active early in the morning, some during midday, and others are most active at dusk (Fukuda et al. 1984). However, published information on the behavior and ecology of the zephyrus hairstreaks is incomplete, and systematic studies on the ecology of these hairstreaks have not been previously conducted. This is partly because adults are largely arboreal, and thus, made difficult subjects for behavioral or ecological studies.

Previously, the senior author observed mating behaviors of one of the sexually dimorphic zephyrus hairstreaks, *Neozephyrus japonicus* (Murray, 1845),

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males of which have metallic green scales on the dorsal surface of the wings, while females have mostly brown or black wings above. Two attempts at courtship, and one copulation event were witnessed, among 22 individuals released in a large cage (Imafuku et al. 2000). Subsequently, the junior authors observed copulation events among wild pairs of *N. japonicus*. Their results were reported at the meetings of the Lepidopterological Society of Japan from 2000 to 2002. Since then, we have conducted a systematic investigation of mating and related behaviors of a wild population of *N. japonicus*. Herein we present the results of those studies, including details of mating behavior from the initiation of courtship to final copulation, along with information on diurnal activity, circling and chase flights, and experimental results on male responses to female models.

MATERIALS AND METHODS

Study area

This study on the behavior of *Neozephyrus japonicus* was conducted in a small wooded area in Ryugasaki City, Ibaragi Pref., Japan (35°55'N 140°10'E), during the butterfly's adult flight season, from the end of June to July, 2000 to 2003. The wooded area was divided

by a narrow lane into two sections; one composed of tall (10-15 m) alder trees, *Alnus japonica* Steudel, and the other composed of willow trees (4-6 m), including *Salix subfragilis* Andersson and *S. chaenomeloides* Kimura (fig. 1). *Alnus japonica* is a local foodplant for larvae of *Neozephyrus japonicus*. The study site was surrounded by grasses such as the reed *Phragmites communis* Trinius, the goldenrod *Solidago altissima* L., and also by cultivated fields.

Observation of diurnal activity

The number of butterflies observed in flight was recorded every 15 to 60 minutes, from dawn to dusk, by slowly walking along the lane. The air temperature was recorded every 5 minutes with a temperature data logger (Gemini Data Logger; temperature) settled in the willow grove (T in fig. 1). The light intensity was recorded by an illuminator situated in open space (shown with L in fig. 1), and data were stored every 5 minutes in a second data logger (Gemini Data Logger; voltage). These counts were conducted from June 30 to July 2, 2002.

Observation of flight activity using a video camera

These surveys were conducted on 4 days between July 2 and 7, 2002. During the peak time of adult activity, near dusk, many butterflies were observed flying over the canopy and edges of trees, occasionally performing chase flights and circling flights (or the spiral flight described by Davies 1978). To record a detailed temporal sequence of changes in these activities, a digital video camera (Sony, DCR-TRV20) was set at a fixed point (C in fig. 1) to record flying butterflies. The camera remained stationary, and recorded individuals that appeared on the north side of the alder woods. Numbers of butterflies, of circling flights and of chase flights appearing every 10 minutes were recorded from 16:30 to 19:00 hrs. Numbers of butterflies were estimated by treating each individual appearing on the screen, until the time it disappeared from view, as separate individuals. The air temperature and light intensity were recorded with a thermometer and illuminator (Mother Tool, LX-100).

Detailed observations and experiments

In order to document detailed patterns of circling and chase flights, butterflies were recorded with a hand-held digital video camera. Recorded images were then incorporated into a personal computer using "iMovie, 2.1.1" (Microsoft), and flight paths

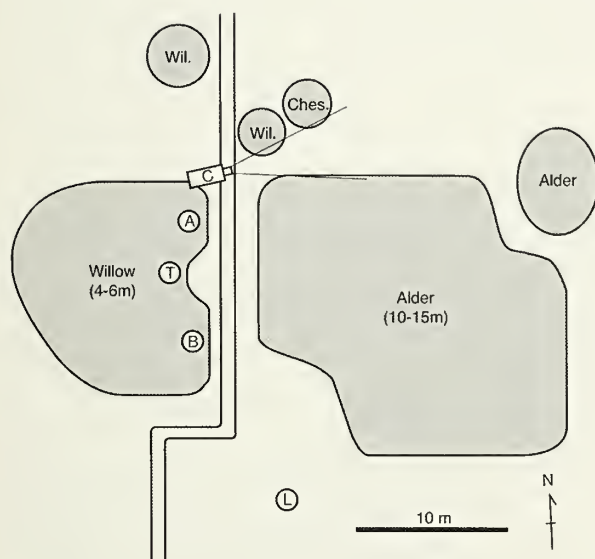


Fig. 1. Study site in Ryugasaki City, Ibaragi Pref., Japan. Patches of willow and alder trees were separated by a path. A thermometer (T) and an illuminator (L) were placed as indicated. A digital video camera (C) was installed for observations of a fixed area, north of the alder grove. A and B indicate sites at which individuals of *N. japonicus* were marked (see Results). Wil. = willow; Ches. = chestnut.

were plotted using "NIH images, 1.62" (courtesy of the National Institute of Health, USA). For drawings in figs. 5 and 6, and in measurements of flight velocity, a reduced scale was calculated by comparing the image size of a butterfly on the computer screen to the average natural size of butterflies collected at the study site. Two arbitrarily determined reference points were also plotted to compensate for changes in images caused by zooming and movement of the camera during recordings.

As chase flights were inferred to occur on participation of a female, two model experiments were performed. In the first experiment ("female model," July 4, 2001), a female hairstreak was allowed to fly, but was tied to the tip of a 3.3 m fiberglass rod with 60 cm of cotton string (#50) secured to her thorax, between the fore- and hindwings. In the second experiment ("female wing model," July 7, 2001), female wings were pasted on both sides of a plastic figure (made from a plastic plate), shaped to mimic a female hairstreak holding its wings open, which was secured to a rod and rotated with a small motor. In each experiment, models were situated in areas where male hairstreaks were active.

In order to determine the sexes of butterflies involved in chase flights, capture with an insect net was attempted. For observations of mating behaviors, binoculars and a video camera were used, and detailed verbal descriptions of various processes were recorded on the latter.

RESULTS

Diurnal activity

Adults of *Neozephyrys japonicus* were most active from 17:00 to 18:00 hrs., just before dusk (fig. 2). This period of peak activity was essentially the same on clear days (e.g., June 30 and July 2, with the highest air temperature over 28°C and the maximum light intensity exceeding 60,000 lux) as it was on cloudy days (e.g., July 1, with temperatures lower than 25.5°C through the daytime and the maximum light intensity lower than 20,000 lux). On clear days, some adult activity was observed in the morning. Shortly before the period of peak adult activity, around 16:00 hrs., females were frequently observed on grasses around the woods, sometimes basking with open wings. As time elapsed, they moved to higher sites in the trees. Around 16:30 hrs., males started to fly over the sides and canopy of the alder and willow groves, and occasional circling flights by two males were performed. As it became darker, chase flights occurred, in which some butterflies appeared to be rapidly chasing other

individuals. With increasing darkness, numbers of flying hairstreaks decreased, and no butterflies were observed by 19:30 hrs.

Evening flight activity

Observations recorded with the fixed video camera during the evening period of peak activity are shown in fig. 3. Flying butterflies first appeared at 16:55 hrs., when the light intensity was 13,000 lux, and numbers of flying butterflies gradually increased with a peak around 18:15 hrs. (fig. 3b). The average time of peak adult activity was calculated to be 18:07 hrs. The light intensity at this time was about 4,000 lux. After this time, the number of flying butterflies gradually decreased.

Circling flights started to occur as number of flying butterflies increased, and continued until flight activity ended (fig. 3a). The frequency of chase flights

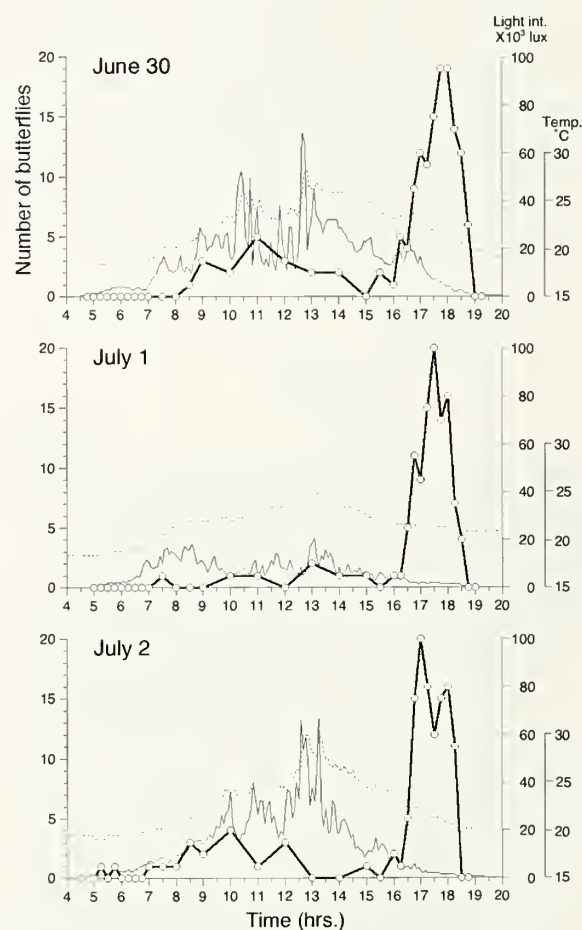


Fig. 2. Changes in the number of flying individuals of *N. japonicus* (thick line) on three days in 2002. Thin and dotted lines indicate light intensity and temperature, respectively. Two days (June 30 and July 2) were sunny, while July 1 was cloudy.

Table 1. Diameter and rotation speed of circling flights in *Neozephyrus japonicus*.

Sample	Sampling time (s)	Diameter (cm)	Rotation speed (rounds/s)
#1	1.30	11	3.8
#2	1.50	12	2.9
#3	2.77	16	2.6
#4	2.93	15	2.4
#5	3.73	19	2.6
#6	2.07	12	3.2
#7	2.63	11	3.1
#8	2.63	20	2.1
#9	3.13	12	3.3
#10	1.97	15	3.1
Average	2.47	14	2.9
Range	1.30-3.73	11-20	2.1-3.8

was greater in the later half of the evening activity period. The greatest average number of circling flights occurred at about 18:05 hrs., while the greatest number of chase flights occurred slightly later, at about 18:20 hrs.

When males were active in circling flights, capturing attempts were made for butterflies straying around a canopy or sub-canopy level, with a result that 4 out of 5 captured individuals were females. Flight behavior of females appeared to be somewhat different than that of males, in that they flew slightly slower, and at a lower altitude.

Circling flights

Circling flights involved two male butterflies, each flying rapidly in a small circle. Most circling flights were completed in a few seconds, whereas some lasted longer. Durations of 46 circling flights observed from July 12 to 17, 2002, are shown in fig. 4. Most circling flights (72 %) were completed within 30 s. The longest circling flight lasted 6 min 18 s. The diameter of the circle varied from 11 cm to 20 cm, with an average of 14 cm (Table 1). Butterflies engaged in a circling flight rotated 2.1 to 3.8 times per second, 2.9 times on average. Thus, their flight velocity in circling flights was calculated to be about 130 cm/s.

A trace of a typical circling flight is shown in fig. 5b. Circling flights were frequently initiated when males happened upon each other, either through random movements (fig. 5a), or through a chase. Rotation direction was not always fixed, and as shown in fig. 5c, sometimes changed. In some cases, a third individual joined into ongoing circling flights. Out of 46 circling flights observed, 14 were invaded by a

third individual. Among these, six were continued by the original circlers with the third butterfly flying away (fig. 5e), six were broken up, and two were continued by the original and the newly arrived third individual (fig. 5f). At the end of circling flights, one of the circlers flew away sometimes, chased by the other (fig. 5d).

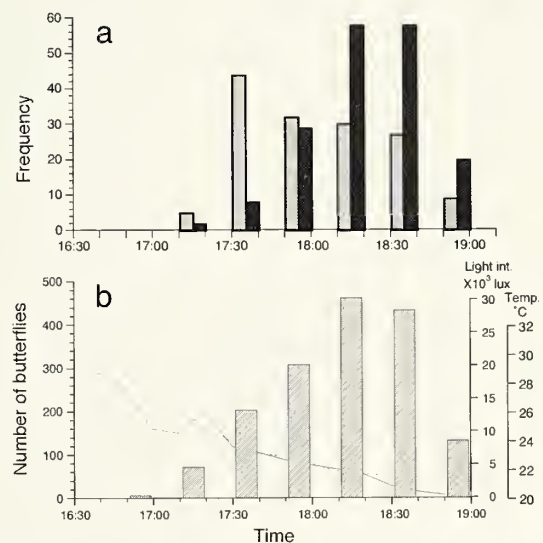


Fig. 3. a. Temporal distribution of circling flights (gray bar) and chase flights (solid bar) during the evening activity period of *N. japonicus* at the study site. b. Temporal distribution of flying butterflies at the study site. Light intensity and temperature are shown with solid and dotted lines, respectively.

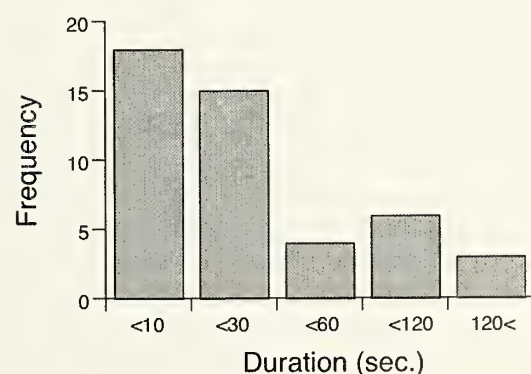


Fig. 4. Frequency of circling flights in *N. japonicus*, plotted against their duration.

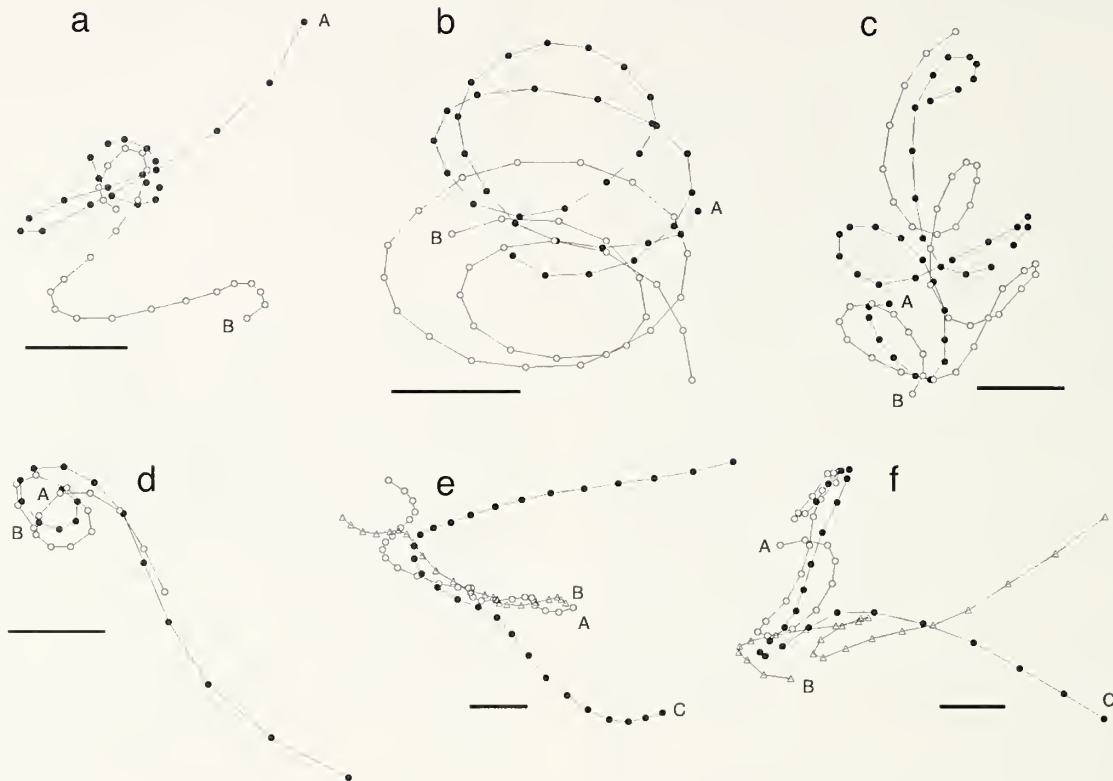


Fig. 5. Traces of flight patterns related to circling flights of *N. japonicus*. In each figure, alphabetical letters (upper cases) indicate individual butterflies and their positions in the first frame of the figure. Each point on the trace line represents the position of the butterfly in successive frames, thus, every 1/30 s. A scale bar below each figure indicates 10 cm. a. Initiation of a circling flight (17:12:55, July 1, 2002). b. Typical circling (18:09:44, July 1, 2002). c. Change of rotation direction; the initial right rotation for the butterfly (left rotation for the observer below) changes to a left rotation (17:48:11, July 1, 2002). d. End of circling, resulting in a chase of one butterfly (A) by the other (B) (18:14:52, July 1, 2002). e. Approach and subsequent retreat of a third butterfly (C) to a circling flight (17:34:21, July 1, 2002). f. Replacement of circlers. One of the initial circlers (A) continues to circle with the invader (C), while the other circler (B) retreats (18:00:37, July 12, 2002).

Residency

Circling flights or spiral flights are usually shown by territorial species (see Discussion). Males of *Neozephyrus japonicus* in the study area did not show clear territorial behavior, but some males repeatedly flew around a specific parts of the canopy. Therefore, residency was examined for our population. Two butterflies at points A and B on fig. 1 were captured and marked with a black felt-tip pen on the undersides of the wings at about 18:00 hrs on June 29, 2002. The butterfly marked at point A was recaptured at the same site and at similar times the following 3 days, until observations at the site were terminated. The butterfly marked at point B was recorded from the same site the following 2 days, but not on the last

day of the study. Thus, butterflies in the study field exhibited a certain degree of residency.

Chase flight

Chase flights were occasionally initiated immediately after circling flights, and sometimes involved multiple individuals (fig. 6d). Some chase flights were very persistent, covering a larger distance immediately after circling flights. Rarely, zigzag flights involving two individuals were observed. A trace of a zigzag flight is shown in fig. 6b, where one butterfly (A) approaches another (F), and proceeds to follow it closely. The chasing butterfly (A) showed a similar turning pattern to that of the butterfly being chased (F), with a delay of 2 to 3 frames (67 to 100 msec).

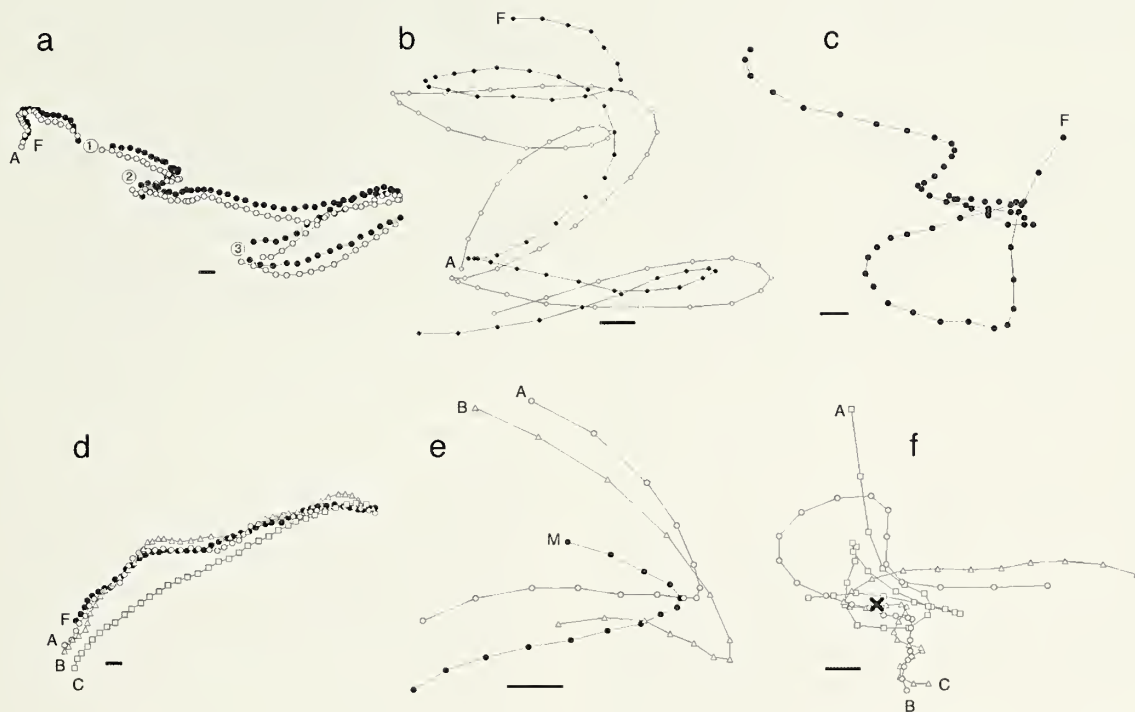


Fig. 6. Traces of flight patterns related to chase flights of *N. japonicus*. Presentations are the same as in Fig. 5, unless otherwise noted. a. A persistent chase of a presumed female (F) by a male (A). Traces were interrupted because of tree branches; 12, 31 and 24 frames were lacked at circles 1, 2 and 3, respectively. This chase continues at least 5.8 s (17:51:26, July 2, 2002). b. A zigzag flight. A presumed female (F) is chased by a male (A) which approaches from below (17:02:56, July 2, 2002). c. Flight path of the presumed female prior to chase by a male, showing a "swinging" flight. The final point of this figure continues to the start point of figure b (17:02:54, July 2, 2002). d. A group chase. A presumed female (F) is always at the lead. "The male "C" appears in the figure after at the 12th frame (17:22:07, July 2, 2002). e. Chase flight by two males (A & B) to the tied female model (M) (18:28:29, July 4, 2001). f. Simultaneous approach of a solitary male (A) and circling males (B & C) to the female wing model (shown with a cross near the center) rotated by a motor (17:58:03, July 7, 2001).

Zigzag flights observed at the study site are thought to involve the chasing of a female by a male (see Discussion). Prior to the zigzag flight shown in fig. 6b, the presumed female (F) descended from the alder canopy into an open space, where she flew in a swinging flight (fig. 6c).

Occasionally, a hairstreak was observed to approach a circling flight involving two males, which resulted in the chasing of the third individual by the two males that had been circling. In cases such as this, the approaching individual may have been a male (as seen in figs. 5e and 5f), but in several cases it was thought to be a female, because the resulting chase by males was very persistent.

The model experiments sought to test the idea that chase flights are frequently composed of a male

(chasing) and female (leading) hairstreak, and the reactions of males upon identifying a potential female mate. Multiple males were attracted to the "female model" tied with thread, and closely followed her flight when she turned sharply (fig. 6e). In fig. 6e, the chasing male followed the abrupt turn of the tied female with a delay of about 2 frames (67 msec). When the "female wing model" rotated by a motor was revealed at the study site, one or more males were frequently attracted (fig. 6f). It should be noted that males engaged in circling flights were sometimes attracted by both of the models.

Finally, the capture of butterflies engaged in chase flights was attempted, using an insect net. Among each of the three successful captures, one female and one male was involved.

Table 2. Copulation statistics for *Neozephyrus japonicus*

Case	Date	Time	Temp.	Duration	Site (from the ground)
#1	10-7-'00	18:46	24.5°C	-	on an alder leaf at 3.8 m
#2	12-7-'01	18:20	27.5°C	ca. 3:20	on a goldenrod leaf at 1.2 m
#3	15-7-'01	18:20	28.5°C	3:18-21	on a goldenrod leaf at 0.9 m
#4	12-7-'02	18:20	25.5°C	-	on an alder leaf at 4.0 m
#5	15-7-'02	18:13	28.5°C	3:07*	on a willow leaf at 1.8 m
#6	17-7-'03	17:13	21.6°C	3:43-4:27	on an alder leaf in 4-5 m
#7	17-7-'03	17:48	21.6°C	5:12-6:08	on an alder leaf in 4-5 m
#8	18-7-'03	17:22	20.9°C	3:40-4:38	on an alder leaf in 4.5 m

*Pairs were carefully brought to a room (30.0°C) and continuously observed.

Courtship and copulation

During the study period from 2000 to 2003, eight instances of copulation were witnessed (Table 2). Copulation usually occurred on leaves, between 3 to 5 m above ground level. On July 10, 2000, at 18:46 hrs, a chase flight involving four butterflies was broken up when a male and a female split away from the group, and landed on an alder leaf 3.8 m above ground level. Subsequently, the male situated himself at a right angle to the female. About 30 seconds after landing, the male walked toward the female and aligned himself next to the female, in a parallel position, so that they were both facing the same direction. Five to six seconds later, the male curved the tip of his abdomen toward the female's genitalia, and after another five to six seconds, succeeded in connecting with the female, to assume a V-shaped body position. At 18:47, the male straightened his figure, and the butterflies faced opposite directions in a normal end-to-end copulation posture. Then, they remained stationary for several hours. At 4:25 hrs the following morning, the pair was found separated. Anatomical examination of the female revealed one spermatophore in the bursa copulatrix.

On July 15, 2001, a copulation event was witnessed after a pair of hairstreaks landed on a goldenrod leaf 0.9 m above ground level, permitting close observations. Upon landing of the female, the male barely clung to the leaf on which the female normally perched. After the male climbed up the leaf, it approached the female from behind at an angle of 60°. Once the male had oriented himself to be side by side with the female, in a parallel position, he retreated slightly, sharply curving the posterior part of his abdomen to contact her genitalia. About 30 seconds elapsed between the time when the pair landed on the

goldenrod leaf and the time they assumed a normal end-to-end copulation posture.

Pairs of hairstreaks landing together after a chase flight sometimes did not couple. In three such cases (17:45 and 17:55 on July 11, and 18:00 on July 12, 2000) copulation attempts ended in failure when the female flew away, even though in one case the male attempted copulation. In most of the copulation attempts observed, males did not open or flutter their wings. However, on July 12, 2002, one male slightly but rapidly and repeatedly fluttered his wings, while situated next to the female, prior to successful copulation. As shown in Table 2, copulation times observed for *Neozephyrus* varied from about 45 minutes to 3 hours and 20 minutes. To check for multiple matings, the bursa copulatrix of 8 females was examined. Five of these females possessed one spermatophore, one female had two, and two females had three.

DISCUSSION

Activity time

Different species of zephyrus hairstreaks are most active at different times during the day. Previously, *Neozephyrus japonicus* has been described as being most active around dusk (Fukuda et al. 1984), but no detailed observations were presented. Herein, we have documented that the peak activity period of wild *N. japonicus* adults is between 17:00 hrs and 18:00 hrs. These results agree with those of an earlier study on a captive population of *N. japonicus*, where adults remained inactive until 16:00 hrs, and were most active after 17:00 hrs (Imafuku et al. 2000).

Peak periods of activity for some other zephyrus hairstreaks have been determined using quantitative data. As shown by Kôda (1982) for *Chrysozephyrus*

brillantinus (Staudinger, 1887) and by Takeuchi & Imafuku (2005) for *Favonius taxila* (Bremer, 1864), some species are most active during the morning, from 7:00 to 11:00 hrs. Hirowatari and Ishii (2001) showed that *Favonius cognatus* (Staudinger, 1892) is most active during midday, from 10:00 to 14:00 hrs. According to Kôda (1982), adults of *Chrysozephyrus smaragdinus* (Bremer, 1864) and *Favonius orientalis* (Murray, 1875) are most active from 8:00 or 9:00 to 16:00 hrs, with suppression of activity during periods of great light intensity. A bimodal pattern with activity peaks in the morning and evening is known for *Artopetes pryeri* (Murray, 1873) (Kôda 1982), *Antigius attilia* (Bremer, 1861) (Kôda 1982; Hirowatari & Ishii 2001) and *Favonius sapphirinus* (Staudinger, 1887) (Hirowatari & Ishii 2001). As shown by Akiyama et al. (1969) and Hirowatari & Ishii (2001), *Japonica saepestrata* (Hewitson, 1865) is most active during the evening hours. Thus, times of peak adult activity are very different among different species of zephyrus hairstreaks. Species-specific activity times might be explainable in terms of predation pressures and intraspecific mating behaviors.

The evening crepuscular activity of *Neozephyrus japonicus* may be related to predator evasion. Birds are known to be one of the most important predators of butterflies, and their activities usually decline at dusk. Swallows, however, were sometimes witnessed to attack circling males of *N. japonicus* during our observations, and some butterfly specimens collected during the course of this study had "beak marks" (Johki 1985) on their wings. Thus, it seems possible that the time of peak activity for adult *N. japonicus* is situated between the time in the evening when most local bird species become inactive, and when it becomes too dark for hairstreaks to see.

Circling flights

In *N. japonicus*, the diameter of circling flights averaged about 14 cm (Table 1). Apparently, the diameter of circles flown by other species of zephyrus hairstreaks has not been measured. However, Fujii (1982) illustrated flights of *Chrysozephyrus smaragdinus*, *Favonius taxila*, *Iratsume orsedice* (Butler, 1881), and (Hewitson, 1865) in "small circles." In contrast, the diameter of circles flown by another lycaenid, *Holochila helenita* (Semper, 1879), extends up to 1-2 meters (Sibatani 1998). Among nymphalid butterflies, Davies (1978) depicted two individuals of *Pararge aegeria* (Linnaeus, 1758) spiraling in small circles, and Sibatani (1998) observed a co-rotating flight of 20-50 cm in diameter for *Mycalesis gotama* Moore, 1857. Sibatani (1998) also observed *Hypolimnas bolina* (Linnaeus,

1758) flying in a circle with a diameter of 50 cm to 1 meter. Bitzer & Shaw (1979) figured a trace from the flight of a red admiral, *Vanessa atalanta* (L., 1758), flying in an ascending helical path, as large as 9 meters in diameter.

Circling individuals of *N. japonicus* occasionally changed the direction of the spiral, as shown in fig. 5c. Such changes were also observed in circling flights of *M. gotama* (Sibatani 1998). However, two interacting individuals of *V. atalanta* reportedly circled "most often in a counter clockwise direction as seen from below" (Bitzer & Shaw 1979).

As for circling or spiral flights, some functions have been proposed. A contest for occupation of territories by males of territorial species has been widely accepted (Baker 1972; Davies 1978; Bitzer & Shaw 1979; Wickmann & Wiklund 1983; Takeuchi & Imafuku (2005). *Neozephyrus japonicus* was described as a territorial species by Fukuda et al. (1984). The two individuals of *N. japonicus* that were marked during our study and observed for several days persisted in guarding the same perching sites, day after day.

As noted by Sibatani (1989), circling flights are also known for non-territorial butterfly species such as *Holochila helenita*, *Eurema blanda* (Boisduval, 1836) and *Neptis sappho* (Pallas, 1771). This suggests that the behavior is not always related to the defense of a territory, but that it may serve to aid in recognition of potential mates (Scott 1974; Suzuki 1976).

A further possible explanation for circling flights among males of *N. japonicus* could be to attract females. Such a scenario may parallel displays by two males toward a female as seen in manakin birds (Snow 1963; Grzimek et al. 1968), where ornamented males show a specific synchronous dance in front of a female. This idea is discussed in further detail below.

Chase flights

Chase flights between two individuals sometimes attracted the attention of other hairstreaks, and small groups were occasionally involved in chases. Capture of hairstreaks engaged in chase flights revealed that such flights included at least one female. Chase flights were often terminated when two individuals break out of the chase, and land near each other. This often led to subsequent courtship or copulation. Thus, chase flights are thought to represent the pursuit of a female by males, and may be one of the steps in courtship.

Zigzag flights observed in the present study (fig. 6b) seem to be a type of chase flight, where a female is being chased by a male. A similar flight pattern was observed in another zephyrus hairstreak, *Chrysozephyrus smaragdinus* (Imafuku pers. obs.). Males of

C. smaragdinus have brilliant green wings above, and are most active during midday, from 10:00 to 16:00 hrs. Therefore, we could easily determine that zigzag flights were composed of a male and a female. It seems possible that females are exerting some selective choice on males, perhaps as judged through their maneuverability, during zigzag flights.

Courtship and copulation

Courtship and copulation events between pairs of *N. japonicus* were witnessed throughout the peak activity period of adults, around dusk, and usually occurred on vegetation between three and five meters above ground level. The timing and placement of these events may protect coupled pairs of *N. japonicus* avoid diurnal predators, and may help them avoid terrestrial predators, such as centipedes and carabid beetles, through periods of relative inactivity during the night.

Duration of copulation between pairs of *N. japonicus* ranged from 3 to 6 hours (Table 2). This does not largely differ from times observed among individuals of *N. japonicus* in captivity, between 2.5 and 3.5 hours (Imafuku et al. 2000). Scott (1973) summarized copulation times for various butterfly species. Extremes included 10 minutes for *Papilio xuthulus*, two days for some *Parnassius* and *Pieris* species, and among lycaenids, two to eight hours for *Callophrys augustinus* (Westwood, 1852) and 1 hour or more for *Nordmannia ilicis* (Esper, 1779). According to Wiklund (2003), copulation times varied from 10 min in *Coenonympha pamphilus* (Linnaeus, 1758) to a week in *Gonepteryx rhamni* (Linnaeus, 1758).

Multiple matings were confirmed among females of *N. japonicus*. This phenomenon is widespread among butterfly species. Scott (1973) examined females of various butterfly species and found that about 95 % of those species sometimes engaged in multiple matings. Suzuki (1988) studied the number of spermatophores in females of 29 butterfly species, and found that all of them possessed two or more spermatophores, except *Lycaena phlaeas* (Linnaeus, 1761) with had only one. The maximum number of spermatophores found in a single female butterfly was 15 in a female of *Danaus gilippus* (Cramer, 1775). Seventeen papilionid species studied by Matsumoto & Suzuki (1995) included female individuals that had mated more than once, and some females of *Papilio helenus* Linnaeus, 1758 and *P. bianor* Cramer, 1777 had mated 6 times. Thus, the phenomenon of multiple matings seems to be general among butterflies. The function of multiple matings for females is thought to include the production of heterogeneous offspring

(ref. Suzuki 1988), or the acquisition of nutrients by females from spermatophores contents (Boggs & Gilbert 1979).

The function of male coloration deserves further discussion. Since the fittest males in various animal populations are often those who successfully compete for mates (Krebs & Davies 1981), male coloration in sexually dimorphic species may serve to attract or court females. As early as 1874, Darwin (p. 505) proposed this hypothesis when he noted that “when we see many males pursuing the same female, we can hardly believe that the pairing is left to blind chance—that the female exerts no choice, and is not influenced by the gorgeous colours or other ornaments with which the male is decorated.” Scott (1973: 101) subsequently noted that “this places selective pressure on males to develop sexual characteristics to make the unreceptive females receptive, ... This may explain why males have brighter colors...” Rutowski (1985) showed that males of *Colias eurytheme* Boisduval, 1852 with strong UV reflectance patterns were more readily accepted as mates by females than were males with weak or no UV reflectance. However, Silberglied (1984) could not confirm this for the nymphalid *Anartia amathea* (Linnaeus, 1758), in which males preferred colorful females but females apparently exhibited no choice between colorful and colorless males. If male coloration serves to attract or court females, it seems that males should actively display their wings during courtship. During courtship between pairs of the sexually dimorphic lycaenid *Pseudozizeeria maha* (Kollar, 1844), the male’s wings are held wide open, as seen in photos by Wago et al. (1976) and Wago (1978), or may be violently fluttered, demonstrating the conspicuous blue upperside coloration (pers. obs.). However, such behavior was not observed among courting males of *N. japonicus*, although slight fluttering of wings was seen on one occasion. In our study, presumed females of *N. japonicus* were occasionally observed to approach a pair of circling males, resulting in the formation of a chase flight. In such cases, the female may have been attracted by male coloration, but at the moment, no evidence to support this idea has been presented. Further studies on the function of male coloration and of circling flights in *N. japonicus* are needed.

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Feasibility of light-trapping in community research on moths: Attraction radius of light, completeness of samples, nightly flight times and seasonality of Southeast-Asian hawkmoths (Lepidoptera: Sphingidae)

JAN BECK* AND K. EDUARD LINSENMAYER

Dept. of Animal Ecology & Tropical Biology, Biocenter, University of Würzburg, Am Hubland, 97074 Würzburg (Germany)
jan.beck@gmx.net

Abstract: Experimental data and quantitative samples of Sphingid assemblages from tropical Southeast-Asia were analyzed to investigate methodologically relevant topics of light-trapping. Mark-Release-Recapture experiments revealed differences between lepidopteran families in the attraction radius of a light source, but no such differences could be found between 18 species within the family Sphingidae. Attraction radii (for 50% return rate within 5 minutes) were generally below 30 meters, which confirms results from previously published studies. Arrival of Sphingidae individuals at a light source was symmetrically distributed around midnight, and species differed significantly in median arrival time. No evolutionary hypothesis for such flight time differences (such as avoidance of interspecific mating or an effect of body size) could be confirmed from our data. At appropriately chosen sample sites (avoiding dense undergrowth), all-night sampling with a 125 Watt mercury-vapor lamp yielded more than $\frac{3}{4}$ of the expected species richness of Sphingidae in an average of 5-6 sample nights. Seasonality and temporal changes of local assemblages can probably be neglected for samples from largely non-seasonal regions like Borneo if data stem from a relatively short study time of a few years. In conclusion, (1) there are no indications that light trapping 'draws' specimens from distant habitats to the sampling site, (2) we did not find proof that species within the family Sphingidae are differentially drawn to light, which would lead to biases if light-trapping data are used as a measure of relative abundance in the habitat, (3) such biases, on the other hand, probably exist between taxonomically or morphologically more diverse taxa (e.g. for different families), and must be considered for a proper interpretation of results, and (4) light-trapping is an effective means of assessing species composition and relative abundances of Sphingid assemblages in Southeast-Asia, but sampling has to be carried out all night in order to maximize catch size and avoid biases due to different flight times of species.

INTRODUCTION

The use of artificial light sources is a commonly employed technique to attract night-active Lepidoptera for the study of taxonomy, biogeography and biodiversity (e.g. Holloway et al. 2001, Intachat & Woiwod 1999). While neither the physiological mechanism (Spencer et al. 1997, Sotthibandhu & Baker 1979, Hsiao 1973, Bowden 1984) nor the evolutionary significance (e.g. Holloway 1967) of this well-known attraction is known to a satisfying degree, it offers a number of advantages over alternative methods such as torchlight-transects (Birkinshaw & Thomas 1999), baiting with fruits, red wine (Süssenbach & Fiedler 1999, 2000), cheese or shrimp paste (S. Benedick & J. Hill, pers. com.), malaise traps (e.g. Butler et al. 1999), suction traps, rotary traps or other methods of passively sampling the air space (see Southwood

& Henderson 2000).

Light trapping yields a large number of specimens with a minimum of effort (Holloway et al. 2001, Fiedler & Schulze 2004). This is particularly true for automatic light-traps (see Southwood & Henderson 2000 for an overview of designs), which do not even require the presence of the researcher during trapping. However, some groups of Lepidoptera such as Sphingidae, which are the main subject of this study, have a tendency not to enter such traps in large numbers, but settle on the outside and in the perimeter of the light source. A comparison between data from automatic light-traps (Nasir Abd. Majid, pers. com.) and hand-sampling at light (own data) showed a ca. 30-fold higher yield for the latter method in lowland Borneo (see also Axmacher & Fiedler 2004, Brehm 2002). Thus, for the rest of this article, the term 'light trapping' refers to attracting moths with light, but sampling them by hand or net. Light can be assumed to sample the community more 'neutrally' than traps baited with food or pheromones, where specializations are more likely to occur. Last but not

* Corresponding author

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least, light trapping allows sampling and killing most specimens relatively undamaged, an important requirement for precise species identification, which is not met by many 'passive' sampling techniques such as malaise or rotary traps.

On the other side, a number of objections to light trapping have been put forward, and Lepidopterists regularly face skeptic criticism by journal reviewers when publishing light-trapping research. The unresolved question of why moths actually come to light (see above for references) might further erode the scientific credibility of the method. The main arguments against light trapping in community ecology (see also Schulze & Fiedler 2003, Brehm 2002 for a more detailed discussion), as well as common responses to these arguments, are:

1) Light traps sample communities selectively rather than randomly. Besides measuring activity rather than relative abundance (see e.g. Wolda 1992, Simon & Linsenmair 2001), not all species are attracted to light to the same extent (Bowden 1982, Butler et al. 1999). Some species of hawkmoth are rarely or not at all attracted to light, but can be caught in numbers by other methods (e.g. Butler et al. 1999, Kitching & Cadiou 2000). Some species seem to be attracted only in parts of their range (e.g. *Daphnis nerii* comes to light in Africa, but not in Asia; I.J. Kitching, pers. com.). Females are generally rarer in light catches of Lepidoptera than males (see e.g. Brehm 2002 for data), which might reflect differences in activity as well as in attraction to light between the sexes. Janzen (1984) described arrival patterns of neotropical Sphingidae and Saturniidae at light and hypothesized on behavioral mechanisms leading to differences between taxa, sexes and age groups. Thus, it can be suspected that relative abundances of species at light are distorted by differential attraction to light and different levels of flight activity. While these potential problems are undeniable, their actual effect on the results of studies on the community ecology of moths remains to be quantified. Light trapping has often been proven to produce readily interpretable and ecologically meaningful results in studies on the biodiversity of Lepidoptera (e.g. Holloway 1976, Schulze & Fiedler 2003, Fiedler & Schulze 2004). Furthermore, the constraints of light trapping are shared with any other comparable sampling method (Schulze & Fiedler 2003, Southwood & Henderson 2000).

2) The effective attraction radius of light sources might be so large that moths are drawn from other habitats to a sampling site. Measurements of the attraction radii of light revealed distances of 3-250 meters (depending on study method and species; Muirhead-Thompson 1991, Bowden 1982), but attraction radii

are probably smaller than 30 meters in most situations for 'normal' light sources in entomological research (Butler & Kondo 1991, Muirhead-Thompson 1991). Furthermore, studies on the stratification of moth communities in the forest produced clear community differences between strata at height differences of 20-30 meters (e.g. Beck et al. 2002, Schulze & Fiedler 2003, Beck & Schulze 2003, using 15 Watt blacklight sources). Thus, while this is a common point of criticism, there is actually little indication that 'drawing' specimens to light from distant habitats really undermines the interpretability of samples.

3) The abundance of specimens at light is influenced by weather, lunar light and vegetation. While the effect of vegetation density around a sample site might be overestimated (Schulze & Fiedler 2003), effects of moonlight and weather (temperature, rain, fog, wind) have been clearly documented and discussed (e.g. Persson 1976, Muirhead-Thompson 1991, Holloway et al. 2001, Intachat et al. 2001, Yela & Holyoak 1997, McGeachie 1989, Brehm 2002). Generally, warm, moist and moonless nights produce highest specimen counts (as has been already noted by R. A. Wallace in 1869, pp. 95-97). Thus, raw abundances at light can never be used as reliable indicators of absolute population sizes in a region, but must be adequately 'converted' into figures which are comparable across samples with regard to the initial question of a study (Southwood & Henderson 2000).

Different light sources (power, wavelength) might also influence sample size and species composition (though this is mainly anecdotal; see Brehm 2002), as does the time of the night during which a trap is operated (e.g. Schulze 2000 found a steady decline in *Pyraloidea* specimens during the first 3 hours of the night in samples from tropical Borneo).

In an attempt to add new quantitative data to this discussion, two sets of questions were experimentally investigated in Sphingidae and other lepidopteran families in Southeast-Asia:

1) What distances of light attraction can we observe under 'real life' research conditions in a tropical habitat? This is particularly interesting for the Sphingidae - very large and extremely fast- and far-flying moths, which might thus be expected to exceed known figures of light attraction radii.

2) Is there evidence for differences in the attraction radius a) between Lepidoptera families with largely differing size, body shape and flight ability, and b) between species of the family Sphingidae? Such differences would be a clear indication that relative abundances of moths at light might present a distorted picture of real abundances, even if species which do not come to light at all (e.g. largely diurnal taxa such

Table 1: List of sampling sites in north-eastern Borneo where release experiments were conducted. Note that latitude and longitude are given in metric format. Additional sampling sites which were re-sampled and used for assessments of seasonality are both on canopy platforms in primary dipterocarp forests at Danum Valley (DV1 - N4.96°, E117.80°, Elev.: 220m a.s.l.), and at Poring Hot Springs in Kinabalu Park (POR1 - N6.04°, E116.70, Elev. 570m a.s.l.).

Site	Nights	Released	Latitude moths	Longitude	Elevation	Habitat a.s.l. [m]	Region
CRO1	9	285	5.44°	116.08°	1170	Ridge with road & planted banana fields, overlooking PF valley & mountains	Crocker Range Park
DV3	5	34	4.96°	117.86°	220	selectively logged (1988), opening along road	Danum Valley
DV4	6	134	4.97°	117.84°	340	selectively logged (1988/89), along road overlooking valley	Danum Valley
POR8	14	1.127	6.03°	116.77°	350	Local agricultural area near village	Poring Hot Springs

as *Macroglossum*) were not considered.

Furthermore, sampling data were analyzed to assess answers to the following general problems of sampling tropical insect populations:

3) What percentage of a local tropical community of hawkmoths can be sampled in a short-term light trapping program? While this question is not particular to light trapping but to any time-constrained ecological study, it is an important background figure to interpret light trapping results.

4) How does the nightly trapping time influence specimen numbers and species composition of samples? It has been suggested (e.g. Kitching & Cadiou 2000, Diehl 1982) that certain species can only be successfully caught at certain times of the night, but so far no quantitative data for whole local assemblages were available.

5) How does seasonality or other temporal change in the Sphingid assemblages of wet-tropical Borneo affect the credibility of results from short-time sampling of local assemblages? While it is often inferred from the climatological stability of tropical habitats that seasonal changes in communities are minute compared to temperate regions, significant effects of weather and season (mostly defined by rainfall) on insect populations have been shown (e.g. Schulze & Fiedler 2003, Süssenbach 2003, Intachat et al. 2001, Novotny & Basset 1998, Wolda 1978, 1988, Wolda & Flowers 1985, Tanaka & Tanaka 1982, Kato et al. 1995, Smythe 1985). Such effects are often ignored in ecological studies in the tropics, as time and logistic constraints do not usually allow for year-round, long-term sampling.

METHODS

a) Field methods

Attraction radius experiments

During two periods of field work in 2001/2002 and 2003, four suitable sampling sites in north-eastern Borneo (Sabah, Malaysia; see Table 1 for details) were chosen for release experiments. Site characteristics that influenced their choice were a high yield of Sphingid specimens (known from previous sampling), overall favorable logistic conditions and the existence of a straight stretch of logging road of at least 120 meters length. A generator-powered mercury-vapor bulb (125 Watt) was placed inside a white, cylindrical gauze-‘tower’ with a height of approximately 1.7 meters from the ground. Sampling was carried out in the period of reduced moonlight from a week before new moon until a week after new moon to maximize catch size. Nightly sampling was carried out from ca. ½ hour after sunset until ½ hour before sunrise, except if logistic problems made this routine impossible.

All arriving Sphingidae were hand-sampled from the light or nearby vegetation (<ca. 3 meter radius), measured (forewing-length), identified (Holloway 1987, D’Abrera 1986, Kitching & Cadiou 2000), and marked individually with a waterproof felt-tip pen on the dorsal forewing. Rare species were either killed and taken for closer taxonomical examination or stored inside the gauze cylinder for release at dawn, whereas common species (c. 14 specimens, see Table 2) were used for this study and released from random-

Table 2: List of all 24 species or *PU*s (1580 individuals) that were included in the release experiments. 18 species belong to the family Sphingidae, five species to the Geometridae and one to the Noctuidae. Some of the non-Sphingid *PU*s could not be reliably determined under field conditions and might refer to any of the species listed in the right column.

Family	Species	Individuals	Comments
Sphingidae	<i>Acherontia lachesis</i> Fabricius	42	
	<i>Acosmeryx anceus</i> Stoll	16	
	<i>Acosmeryx shervillii</i> Boisduval	70	
	<i>Ambulyx canescens</i> Walker	37	
	<i>Ambulyx moorei</i> Moore	38	
	<i>Ambulyx pryeri</i> Distant	49	
	<i>Ambulyx subtrigilis</i> Westwood	20	
	<i>Amphypterus panopus</i> Cramer	19	
	<i>Ceichenena helops</i> Walker	40	
	<i>Daphnis hyppothous</i> Cramer	211	
	<i>Marumba juvenis</i> Rothschild & Jordan	14	
	<i>Megacorma obliqua</i> Walker	20	
	<i>Psilogramma menephron</i> Cramer	147	
	<i>Theretra clotho</i> Drury	112	
	<i>Theretra latreillii</i> W.S. Macleay	49	
	<i>Theretra nessus</i> Drury	184	
	<i>Theretra rhesus</i> Boisduval	260	
	<i>Theretra silhetensis</i> Walker	18	
Geometridae (Ennom.)	<i>Biston</i> 3sp. Leach	31	<i>B. inouei</i> Holloway, <i>pustulata</i> Warren or <i>insularis</i> Warren
	<i>Celerena signata</i> Warren	22	
	<i>Dalima subflavata</i> Felder & Rogenhofer	36	
Geometridae (Geomn.)	<i>Pingasa chlora</i> Stoll	44	
	<i>Thalassodes</i> -complex (24sp.)	34	Genera <i>Thalassodes</i> , <i>Pelagodes</i> or <i>Orothalassodes</i>
Noctuidae (Aganainae)	<i>Asota</i> 4sp. Walker	67	<i>A. plana</i> Walker, <i>albiformis</i> Swinhoe, <i>heliconia</i> Linnaeus or <i>egens</i> Walker
Σ Sphingidae		1346	
Σ Geometridae		167	
Σ Noctuidae		67	

lychosen distances along a logging road (distances in 5 meter steps, from 5 up to 120 meters, at one site up to 130 meters). After preliminary trials moth were transported to the release distance inside a plastic jar (500 ml) immediately after marking and released by turning the jar upside-down without giving the moths an initial flight direction. While this procedure carries the risk of non-directional, panicked flight rather than providing an ideal situation for deliberately choosing a flight direction, it avoided the effect that moths kept for a prolonged period after catching 'cooled down' after handling and often refused to fly at all when released, sitting in the same spot for hours. Catch time, release time and distance, and recapture time at the light were noted for all individuals. Each moth was released only once: after recapture it was stored

inside the gauze cylinder for release at dawn. Recaptures of marked specimens on following nights were not considered at all, but their occurrence at a rate of ca. 5 percent indicates that marking does not harm the moths (see also Beck & Schulze 2000, Beck et al. 1999). One species, *Daphnusa ocellaris*, was excluded from analysis as it was frequently observed trying to escape by crawling rather than by flight after handling (see discussion).

For a comparison between lepidopteran families, several *parataxonomic units* (*PU*s, Krell 2004) from non-Sphingid groups were chosen for their commonness and easy identification under field conditions (Holloway 1986, 1993, 1996). Three of these *PU*s contained several species in a genus, impossible to separate alive and in the field (see Table 2). These considerably

smaller and more delicate moths had to be caught, marked and handled with special care. Specimens which were accidentally injured were excluded from experiments.

Completeness of samples, flight time and 'seasonality' comparisons

Data for an assessment of the faunal completeness of short-time, high-intensity light trapping stem from an extensive sampling program in Southeast-Asia that was carried out from early 2001 to early 2004. Except for the four sites at which release experiments were conducted (see above) all sampling schedules were carried out independently of weather or moonlight conditions, so effects of these factors on abundance or flight time of moths should be randomly distributed. Generally, Sphingidae were hand-sampled (as described above) all night long for three to nine consecutive nights in a block. Median nightly sampling time was 10.2 hours. Sites with samples of less than 20 specimens within the first three nights were ignored. For the purpose of assessing the completeness of the applied sampling procedure we used data for 15 sites in north-eastern Borneo and one in Peninsular Malaysia. Sampling habitats ranged from primary forests through variously disturbed forest types to open, agricultural landscapes, from lowlands up to almost 1500 meters elevation. Sites were generally situated either in open areas or in the forest canopy (platforms or on cliffs or steep slopes) in order to maximize Sphingid catch (see Schulze & Fielder 1997). Four sites in Sabah (north-eastern Borneo) were re-sampled up to four times during the 3 year-study (see Tables 1 & 5, minimum 6 month between re-samples). These re-samples were used to assess effects of temporal change, but were considered as independent samples for the purposes of an evaluation of sample completeness, which raises the sample size to 23 sampling sessions.

At 11 sites in Borneo and one in Peninsular Malaysia, detailed arrival times of all specimens were measured (in 15 minute-steps: data from all sites were pooled for this analysis).

b) Methods of analysis

Return times of the experimentally released specimens ranged from a few seconds to more than eleven hours; about 47 percent of the released moths were not seen again at all during the night of release. Some specimens obviously did not directly return to the light, but flew around in the area and were later attracted to the light source again. Thus, we applied

the rule that only returns within five minutes from release were counted as '*returns*' for analysis, while any later arrivals were considered as '*non-returns*'. From speed measurements (100 meters in less than 20 seconds for several Sphingidae species) and direct observations of flight behavior we concluded that all species should be able to reach the light in that time interval even if they take some time to start or orient after release. Return rates per minute dropped rapidly within the first few minutes and reached a bottom level after about eight minutes (when 50% of all returning moths have come back to the light). Return rates after this point fluctuated apparently randomly (on a level of 0-2% return rate per minute) and probably represent released specimens which did not return directly to the light, but flew around in the area and entered the attractive radius of the light again at some later time, as described above. Preliminary analyses suggested that analysis with a five-minute return criterion yields a higher statistical power than longer return times (i.e., 8 min., 15 min.). After that time directional movements towards the light can probably not be expected any more.

Besides standard statistical procedures, the following methods of analysis were employed:

Loglinear Model

A loglinear model was used to test for influential factors on the frequency of *returns* vs. *non-returns*. Release distances were grouped into six 20 meter classes (5-20m, 25-40m, 45-60m, 65-80m, 85-100m, 105-120m), release distances >120m were not used for this analysis, as they were not available from all sites. A multi-dimensional contingency table, containing the frequencies of *returns* as well as those of suspected influential factors (such as release distance class, species identity), was constructed with all possible interactions between these factors, and then tested against the actual data (for a detailed description of loglinear models see StatSoft 2003).

Logistic Regression

As a second mode of analyzing the release experiment data we used logistic regressions (Trexler & Travis 1993). While carrying the disadvantage that not all data sets can be fitted well by logistic regression (predicting *return/non-return* better than random, see below), they allow assessing attraction radii (as the distance of 50 percent return-probability) in meters, rather than just comparing them on a class level.

The logistic equation (see e.g. Trexler & Travis 1993) was fitted to the *return/non-return* (1/0) data

(original data in 5 meter intervals). Regression values can be interpreted as probability for *return* (StatSoft 2003), the point of 50% return probability (x_i = *turning point* of the logistic regression for species i) is used as a measure of attraction radius. The variance of x_i is calculated from the variance of the regression parameters (b_0, b_1) as

$$\hat{\text{var}}(\hat{x}_i) = (\hat{x}_i)^2 \cdot \left[\frac{\hat{\text{var}}(\hat{b}_0)}{(\hat{b}_0)^2} + \frac{\hat{\text{var}}(\hat{b}_1)}{(\hat{b}_1)^2} \right], i = 1, 2$$

For graphic display, 95% confidence intervals were assessed as $1.96 \cdot (\text{SD}(\hat{x}_i))$. For a more rigorous test of the hypothesis of a difference between two *turning points*, a z-test (StatSoft 2003) was used. Both the loglinear models and the logistic regressions were calculated with the computer program *Statistica 6.1* (StatSoft 2003).

Estimating total species richness

From the distribution of species in discrete samples an estimate of the total species richness at a site can be assessed by several methods (see Chazdon et al. 1998, Colwell & Coddington 1994, Colwell 2000, Melo et al. 2003). Of these, the non-parametric *Chao1*-estimator was used as it has proven robust in pilot studies (Chazdon et al. 1998, Peterson & Slade 1998) and yielded realistic figures in studies on temperate moths (Beck & Schulze 2003, Süssenbach & Fiedler 1999), where the total species richness is much better known than in tropical regions. Assessments of the species diversity of habitats by *Chao1*-estimates are often congruent to those with well established methods like Fisher's α or rarefaction curves (e.g. Beck et al. 2002, Schulze 2000). However, Brose & Martinez (2004) have concluded from simulation studies that in assemblages of species with variable mobility other estimators might perform better. In order to account for this finding, we additionally followed the suggested procedure of finding the 'optimal' estimator for the sample coverage at each site (calculated from the means of *ACE*, *ICE*, *MMMmeans*, *Chao1*, *Chao2*, *1st order Jackknife* and *2nd order Jackknife* estimators; see Brose & Martinez 2004). All species richness estimates were calculated with the computer program *EstimateS 5.01* (Colwell 2000).

The 'False Discovery Rate'-control of Benjamini & Hochberg (1995) was applied to avoid spurious significances due to multiple tests from the same data set, and all results which pass the criteria are marked

with an asterisk (*). However, it was not considered necessary to control analyses of different data sets, even if they overlap or are nested within another (see also Moran 2003).

Phylogenetic independence

Correlations of species' characters might not be statistically independent because of their common phylogenetic history (see e.g. Garland et al. 1999 for a review). The phylogenetic signal in data was tested with a randomization test (1000 runs), using the program *Phylogenetic Independence 2.0* (Reeve & Abouheif 2003, see also Abouheif 1999, Freckleton et al. 2002). Hawkmoth phylogeny was based on an updated version of the systematics in Kitching & Cadiou (2000, I.J. Kitching, pers. com.), allowing for unresolved nodes where applicable. To control for non-independent data, 'independent contrasts' (Felsenstein 1985) were calculated using the computer program *PhyIip 3.61* (Felsenstein 2004; all branch length set to 1 except unresolved nodes, which were set to 0.0001).

RESULTS

1a) Release experiments: Loglinear models

A sample size of 1527 released moths was available for loglinear model analysis. The data structure was not suitable to include all interesting variables (return frequency, distance, species identity, family affiliation, experimental site) into one model. Therefore, certain variables were tested in separate models.

The first model analysis (see box 1) suggests that the research site had no influence on return frequencies, so data from different sites were pooled for all further analyses. Family affiliation of specimens had a clear influence on return frequencies (see 2nd model in box 1, figure 1), while for 18 species within the family Sphingidae no significant effect of species identity on return frequencies could be found (3rd model in box 1). All analyses show a significant effect of release distance on return frequencies. This was expected, since the frequency of returns should decrease with diminishing light intensity at larger release distances.

1b) Release experiments: Logistic regression

For the three families, as well as for twelve Sphingid species, logistic regression models could be constructed, while for six Sphingid species the models did not pass the χ^2 -test of a better-than-random prediction of the data. These species were consequently excluded

Box 1: Loglinear models**Model 1:** "Effects of research site" [site (4) x return (2) x release distance (6)] (*N*=1527)

Model 1	² (max. likel.)	df	p
Start model with 3 double-interactions	15.807	15	0.395
Best model (return-dist., site-dist. interactions)	18.715	18	0.410

Already the optimized model does not contain interactions of *research site* & *return frequency*.

Conclusion 1: No effect of site on return frequencies.

Model 2: "Effects of family" [*family* (3) x *return* (2) x *release distance* (6)] (*N*=1527)

Model 2	² (max. likel.)	df	p
Best model: 3fold- interaction fam. x return x dist	0	0	1
Exp. model 1: no 3-fold, but all 3 2-fold interactions	20.399	10	0.026*
Exp. model 2: no 3-fold and no fam.-return interaction	54.360	12	<0.0001*

The exclusion of the 3-fold interaction ("family influences distance-return interaction") leads to a significant difference between model predictions and real frequencies in data. Further exclusion of the family-return interaction brings another significant loss of predictive power of the model ($\chi^2_{df=2}=34$, $p<0.0001^*$).

Conclusion 2: Families have different return rates from different distances, i.e. different attraction radii. Beyond that, families differ in overall return rates (exp. model 1 *vs.* 2).

Model 3: "Effects of species" [species (18) x return (2) x release distance (6)] (*only Sphingidae*, *N*=1352)

Model 3	² (max. likel.)	df	p
Start model with 3 double-interactions	68.625	85	0.903
Best model (only return-dist interaction)	169.99	187	0.809
Exp. model without any interactions	298.73	192	<0.0001*

Conclusion 3: No effect of species identity (within the Sphingidae) on return frequencies is evident; already the optimized model does not include species. The exp. model only proves the essentially expected effect of release distance on return rates – otherwise the experiments would have been senseless.

from analysis. Figure 2 shows an example of a logistic regression for one species, figure 3 plots the attraction radii of the light (measured as the 'turning points' of the regression) and their estimated confidence intervals for the hawkmoth species.

On family level, 50% return rates vary between ca. 10-13 meters for Sphingidae and Noctuidae, whereas negative values for Geometridae were calculated due to very low overall return rates for *Pingasa* (5 returns of 44 releases) and particularly the small Geometrinae of the *Thalassodes*-group (5 of 34). Possibly handling effects have affected results in this very delicate group, although no obvious inability of flight was observed. The other Ennominae species showed attraction radii comparable to that of Sphingidae or Noctuidae (data not shown).

Turning points for Sphingid species vary between

26 meters and negative values (for species with very low return rates). Confidence intervals are large and indicate a high, unexplained variability in return behavior. For two species no variance of parameters could be calculated due to the structure of the data matrix. Maximum confidence estimates range up to 60 meters, which is still a value in reasonable boundaries of the literature for attraction radii of light (see e.g. Muirhead-Thompson 1991). No significant differences between species could be found for the 10 species for which testing was possible. Turning points of species do not correlate with the average body size of the species ($N=12$, $r^2=0.031$, $p=0.588$), whereas Fiedler et al. (unpublished) have found effects of body size on return rates in other, temperate Lepidoptera families.

Thus, the results obtained by logistic regression

confirm the analyses with the loglinear models.

2) Completeness of samples

During an average of 5-6 nights per sampling session, an average of more than $\frac{3}{4}$ of the *Chao1*-expected 'true' species richness could be collected (see Table 3 for details). Sampling success is weakly related to the number of sample nights as well as the number of sampled specimens, but not to observed species richness or diversity (as Fisher's α ; see figure 4 for test details).

Measurements of sampling success based on six other selected estimators of species richness (see methods) yield mostly quite similar figures, although Kendall's concordance coefficient for the seven estimators is surprisingly low at 0.173 and a Friedman-ANOVA indicates significant differences between estimator ranks ($N=23$, $\chi^2_{df=6}=23.85$, $p<0.001^*$).

An application of the method suggested by Brose & Martinez (2004) lead to the use of *ICE*, *1st* and *2nd* order *Jackknife* estimators, depending on the sample coverage for each site. However, overall results are very similar to *Chao1*-based estimates and indicate an average sample coverage of 77.3 percent.

Comparison with other samples from the region

In Table 4 the species richness (observed and expected) of the 23 standardized samples is compared to a combination of data from our own samples, published literature (Chey 1994, 2002, Holloway 1976, Tennent 1991, Zaidi & Chong 1995, Schulze 2000) and unpublished collections (Azmi Mahyudin and J.D. Holloway, pers. com.). These data vary in the use of different light types, sampling regimes and specimen numbers (local samples <20 specimens were not considered). Observed local species richness ranges up to 50 species (see figure 4: only samples with >1000 specimens contained over 40 species). Thus, the highest *Chao1*-estimate of 68 species (Table 4) is still in a realistic range. The slope of the data in figure 6 suggests that this may be close to the maximum local species richness that can be found by light-trapping in this region. Schulze et al. (2000) reported 59 night-active Sphingidae species from a compilation of data from several sampling sites within Kinabalu Park, Sabah. Higher records of local species richness in Southeast-Asia can probably only be found from continental regions (e.g. 67 species from year-round sampling on a site in northern Vietnam, T. Larsen, pers. com.), where regional species richness is higher than in insular Southeast-Asia (Beck & Kitching 2004).

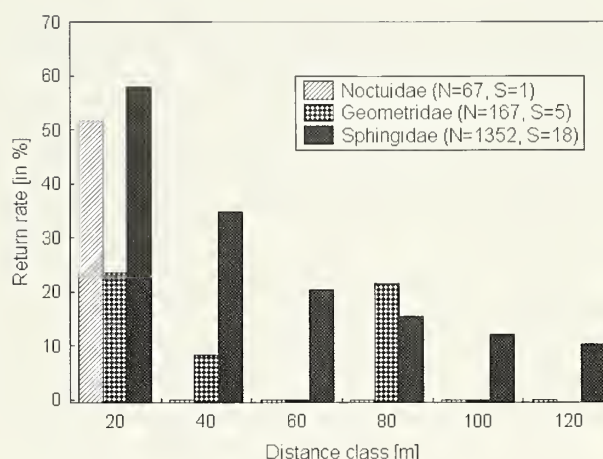


Figure 1: Return rates within 5 minutes (in percent) of three Lepidopteran families from six release distance classes (note that 'Noctuidae' contains only the genus *Asota*, see Table 2). Loglinear contingency table analysis (see box 1) indicates significant differences in return rates between the families.

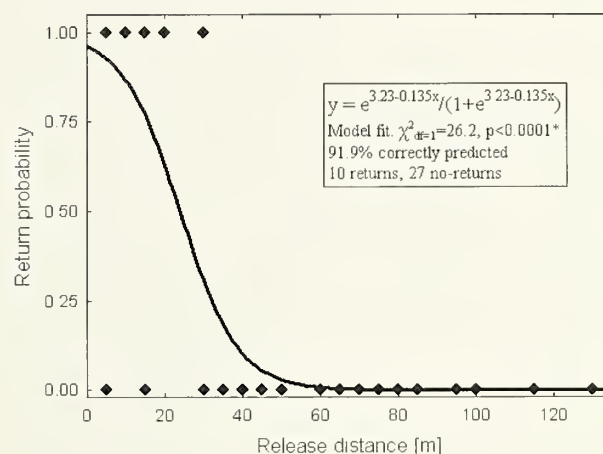


Figure 2: Exemplar logistic regression fit of the binary data (*return/non return*) for the Sphingid species *Ambulyx canescens* ($N=37$). Regression values (y-axis) range between 0 and 1 and can be interpreted as probability for 'return'. The 'attraction radius' (turning point of the regression curve = 50% return probability) is estimated at 23.9m for this species. Note that several data points may lie on the same position, which are not shown in the graph but influence the slope of the curve.

3) Flight time during the night

Figure 7 shows the distribution of arrival times of 1450 hawkmoths at 6 sample sites. Arrivals are clearly

Box 2: Z-tests for differences of logistic regression turning points (a) of families (b) of the most extreme species. Values in bold indicate significant differences ($z > 1.96$, $p < 0.05$).

a)

<i>z-value</i>	Sphingidae	Noctuidae
Noctuidae	-0.664	
Geometridae	2.173	2.418

b)

<i>z-value</i>	<i>A. shervillii</i>	<i>T. latreillii</i>	<i>T. rhesus</i>	<i>Asota 4sp.</i>
<i>T. latreillii</i>	1.469			
<i>T. rhesus</i>	1.024	-0.956		
<i>Asota 4sp.</i>	0.908	-1.112	-0.307	
<i>D. subflavata</i>	1.790	-0.295	1.094	1.436

Table 3. Mean values of 23 sampling sessions for the number of individuals (N), species (S), sampling nights, as well as the *Chao1*-estimate of true species richness (Colwell 2000), the proportion (in percent) of observed/estimated species richness (% S_{obs}), and the mean number of individuals per sampling night. The median is also given where distributions deviate from normality (KS-test, $p < 0.05$).

	Mean \pm SE	Median	Min.	Max.
N	220.9 \pm 48.5	116	25	847
S_{obs}	22.1 \pm 1.5		10	38
Nights	5.5 \pm 0.3		3	9
Chao1	30.1 \pm 2.5	28	14	68
% S_{obs}	75.9 \pm 3.2		37.9	94.4
N/night	35.9 \pm 6.5	26.2	6.2	121

Table 4. Species richness (observed and estimated) of local samples from Borneo and Peninsular Malaysia. See text for data sources of "all data".

	Samples	Mean	SD	Min	Max
S_{obs} (own)	23	22.1	7.4	10	38
Chao1-est (own)	23	30.1	12.1	14	68
All data S_{obs}	60	20.2	10.4	5	50

symmetrically distributed around midnight, with a steep rise in specimens in the third hour since sunset, and a decline after eleven hours. This is in marked contrast to smaller moths in Borneo or in temperate

regions (e.g. Thomas 1996, Schulze 2000, and own observations), which considerably decline in numbers after 2-3 hours past sunset.

Flight times clearly differ between species (figure 8). Median flight times also differ between Sphingid subfamilies, with Smerinthinae flying on average earlier in the night and Sphinginae later (KW-Anova: $H_{df=2} = 20.27$, $p < 0.0001^*$). However, median values for subfamilies are still quite tightly clustered around midnight (Smerinthinae 6h, Sphinginae 7.5h past sunset). Median arrival times also differ between sites (KW-Anova: $H_{df=11} = 130.8$, $p < 0.0001^*$), which is most probably the effect of different moonlight and weather conditions. Over the range of sample sites, however, these differences are leveled out as figure 7 shows a very symmetric distribution.

Assuming flight times are adaptive, two hypothetical factors can be tested with for an influence on flight time differentiation: a) Avoidance of mating in closely related taxa might be a reason for differences in activity patterns. Species within genera should have less flight time overlap than average species couples. b) With decreasing temperatures during the night, larger species can maintain their flight muscle temperature, hence their agility, more easily than small-bodied species.

Pianka's niche overlap of flight times was calculated for the 20 most commonly recorded Sphingidae species [$N_{per\ sp.} > 12$] as well as for intra-generic comparisons [$N_{per\ sp.} < 10$] within the genera *Ambulyx* [5 spp.], *Theretra* [4 spp.] and *Acosmeryx* [2 spp.] (see Southwood & Henderson 2000, computed with Programs for Ecological Methodology, Kenney & Krebs 2000). Mean values of niche overlap range around 0.57 for all Sphingidae and > 0.7 for the intra-generic comparisons. Thus, no indication for a lower overlap for within-genera comparisons was found. There is a tendency for smaller species to fly earlier than large species ($N = 49$, Pearson's $r^2 = 0.109$, $p = 0.021$; body size was measured as mean forewing length, which is a good surrogate for body mass within a group of similar body architecture; Loder et al. 1998, Schoener 1980). However, a clear phylogenetic signal was detected in body size data (randomization test: $p = 0.001^*$ for phylogenetic independence), whereas no signal was detected in flight time data ($p = 0.430$). A correlation of independent contrasts for body size and flight time is not significant ($N = 48$, $r^2 = 0.017$, $p = 0.376$), nor is a correlation of contrasts for body size with 'raw data' for flight time ($N = 48$, $r^2 = 0.002$, $p = 0.769$), using contrasts for a neutral, star-like phylogeny (see also Rheindt et al. 2004 for methods). These analyses indicate that the weak relation between flight time and body size (see above) must be considered spurious under the

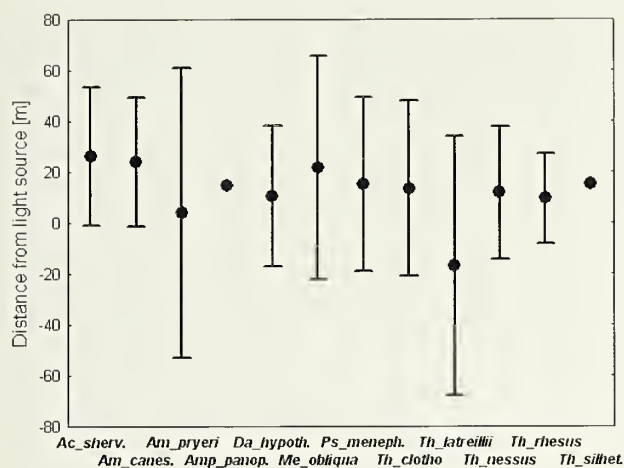


Figure 3. 'Turning points' of logistic regressions for Sphingidae species, which indicate the distance of 50 percent return-probability ($\pm 1.96SD$) after experimental release. No significant differences can be found between the species.

above described assumptions.

4) 'Seasonality' and temporal change

Comparisons of the 'within-habitat' diversity of re-sampling sessions (figure 9) showed a remarkable constancy of measures; only at one site (CRO1) a significant change in diversity could be observed, even though the species inventory in both samples was identical (Table 6). No influence of 'seasons' (see Table 5) on diversity differences could be observed, indicating that changes in the structure of hawkmoth assemblages are either random or directional in a longer time scale than one year (Beck et al., 2006). Measures of between-session similarity of sampled assemblages are relatively high, particularly for NESS-indices (Grassle & Smith 1976) which are not biased (towards lower values) by incomplete speciesinventories as Sørensen-indices are (Southwood & Henderson 2000). If common species are weighted high for calculation of $NESS(m=1)$, it seems that primary forest sites (DV1, POR1) are more stable than disturbed sites. This pattern, however, breaks down if rare species are weighted higher at $m=21$. All $NESS(m=21)$ -values are >0.82 for within-site comparisons of sessions (as e.g. in Novotny et al. 2002). Multidimensional Scaling (figure 10) of $NESS(m=21)$ -values illustrates that faunal differences between seasons are mostly smaller than those between sites. The sampled assemblages were tested for spatial and temporal differences (see Table 5 for classification) by the randomization test

Analysis of Similarity (ANOSIM), using PRIMER 5 (2002). In one-way designs, significant effects could be found between sites (Global $R=0.711$, $p=0.001^*$), but not between seasons (Global $R=0.043$, $p=0.552$) or sampling year (Global $R=0.026$, $p=0.397$). Furthermore, in various two-way designs (including nested designs) no temporal effects (season or year) could be found.

Relative abundances of sampled species were correlated to each other (Table 7) to assess how well sampling in one session reflects the rank order of species in other sessions at a site. All relevant correlations are highly significant, though R^2 -values are not particularly high. Within-site correlations have significantly higher R^2 -values than between-site correlations (t -test: $t_{df=53}=7.47$, $p<0.0001^*$).

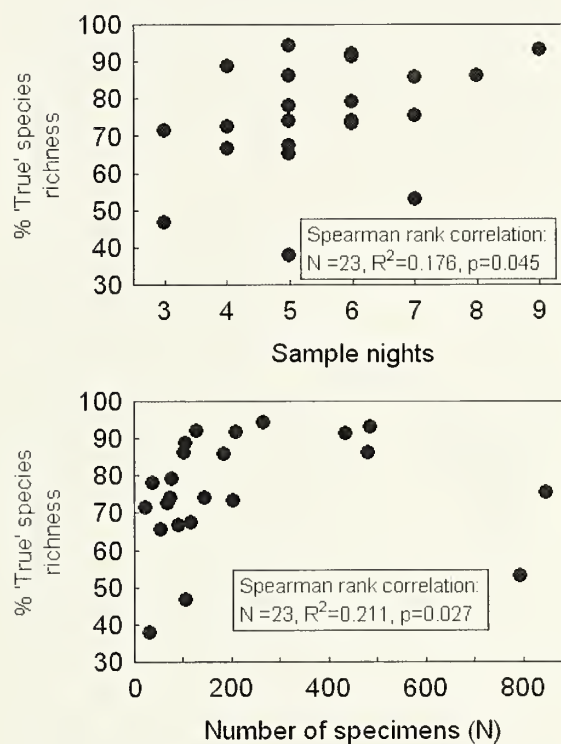


Figure 4. Correlations between the number of sample nights (upper graph) and the number of sampled individuals (lower graph) and the percentage of sampled 'true' species richness (based on *Chao1*-estimates, Colwell 2000). Each dot refers to a different sampling session, not to sub-samples from the same sampling session. No correlations were found with the observed number of species (S_{obs} : $N=23$, $R^2=0.012$, $p=0.614$) and the species diversity (Fisher's α : $N=23$, $R^2=0.084$, $p=0.179$).

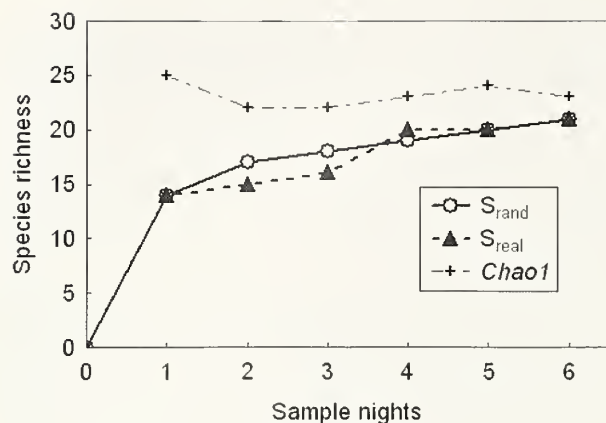


Figure 5: Exemplar species accumulation curves for a 'good' sampling site at Danum Valley, Borneo (DV1-I): After 6 nights of sampling, 21 of 23 estimated species were caught (91.3% sampling success). S_{rand} is smoothed by a 100-fold randomization of the sample night order (Colwell 2000), $Chao1$ is the estimate of total species richness at the respective number of (randomized) sampling nights. The *MMMeans* estimator (Colwell 2000), which fits an asymptotic curve to the randomized species accumulation curve, yields an estimate of 22 species for this site. The total number of specimens at this sampling session was 437.

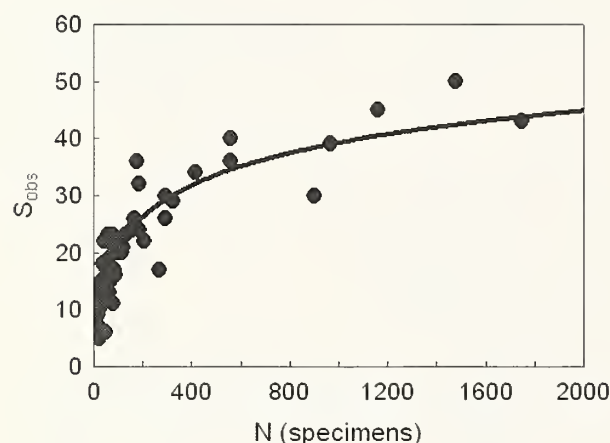


Figure 6: Observed species richness of Sphingidae as a \log_e -function of the number of sampled specimens for 60 local light-trapping samples from Borneo and Peninsular Malaysia (see text for data sources). The data are significantly correlated ($N=60$, Pearson's $r^2=0.839$, $p<0.0001^*$).

DISCUSSION

Attraction radius of light sources

In the experimental part of this study we showed

for 18 species of Sphingidae, as well as some species of the Geometridae and Noctuidae, that the effective attraction radius of a 125 Watt MV-lamp is indeed relatively low with mean attraction distances below 30 meters. This confirms what most previous studies found with different methods, species and habitats (e.g. Muirhead-Thompson 1991, Bowden & Morris 1975, Onsager & Day 1973, Plaut 1971, Meineke 1984, Kovács 1958). Even for hawkmoths, which probably form the upper limit of lepidopteran flight strength and speed, there is no indication that light trapping draws moths from distances so great that investigations on local habitats were 'polluted' by specimens from far away. Occasionally specimens were found at light sources far from their typical habitat (e.g. on ships far off the nearest coast; I.J. Kitching, pers.com.), but there is no indication whatsoever that such specimens were artificially drawn out of their natural habitat by the light. Due to dispersal and migratory behavior some few individuals of a species will always show up away from its breeding habitats, but such 'strays' are not *per se* an artifact of sampling.

Differences between taxa

A comparison between families with considerably different body sizes and shapes revealed significant differences in return behavior and attraction radius. Fiedler et al. (unpublished data, pers. com.) found in similar mark-release experiments in Germany that body size has a significant effect on return rates of Geometroidea (though not in other taxa). Therefore, results of light trapping studies from taxonomically and/or morphologically very diverse samples must be viewed very carefully, as relative abundances at the light might not reflect relative abundances under natural flight conditions across all taxa. Within the relatively uniform taxon Sphingidae, on the other hand, comparisons of 18 species did not show any non-random differences in return behavior despite a considerable sample size (over 1300 released specimens, see Table 2). While it is known that some differences between species must exist (e.g. some species do not come to light at all; Butler et al. 1999 found substantial differences between blacklight and malaise traps for three North American hawkmoth species), these differences might often be diluted beyond significance by a high variability in attraction radii (see below) during natural trapping conditions. It might be argued that in this study the concentration on relatively common species (for the obvious reason of attaining sufficient sample sizes) might have neglected systematic differences between common and rare species. Generally, a lack of an effect is never proof of

its non-existence, but there is presently no indication to assume a systematic difference in attraction radius between rare and common species.

The species-abundance distributions in a large number of light-trapping samples of hawkmoths from Southeast-Asia fit the lognormal distribution very well (Beck, 2005). This or similar mathematical distributions have been found in samples of a large number of organisms (e.g. Tokeshi 1993), including light-trap samples of moths (e.g. Robinson 1998) as well as data from sampling procedures that are beyond any doubt free of sampling errors (e.g. counting tree seedlings in sample squares, Hubbell 2001). If the lognormal and related distributions have any biological significance (e.g. Hubbell 2001, Hengeveld & Stam 1978) and are not merely a statistical characteristic inherent to any heterogeneous data set, then massive biases of light trapping would have distorted this relationship for night-active Lepidoptera sampled in this way.

High variability in data: A methodological artifact?

The release experiments revealed a large variation in return behavior that was also evident from observations during field work. While some specimens were seen flying in a straight line towards the light after release at distances of up to 130 meters, other specimens did not return at all. The failure to find species-specific differences in light attraction might be attributed to this variability rather than homogenous measures of attraction (see e.g. figure 3). Therefore it is a crucial question for the interpretation of results to what degree such variation might be caused by handling effects or other problems of the experimental design. Obvious handling effects could repeatedly be observed in *Daphnusa ocellaris*, which walked away after release rather than trying to fly, and was consequently excluded from all analyses. However, it was not completely surprising to find odd behavior in this species, as it is an 'unusual' hawkmoth in a number of other behavioral traits: In Borneo, it is the only species that is frequently encountered in the undergrowth of the forest, while all other species tend to fly in the open airspace above the tree canopy (Schulze & Fiedler 1997). Furthermore, its relatively small thorax makes it considerably weaker in beating its wing than species of comparable size (pers. obs. during handling). The observed behavior can probably be interpreted as a predator escape tactic after an unsuccessful first attack of a bat. In no other Southeast-Asian hawkmoth species was such behavior observed.

Predation by bats around the light was high, and occasionally released moths were caught by bats just before returning to the light (pers. obs.). While

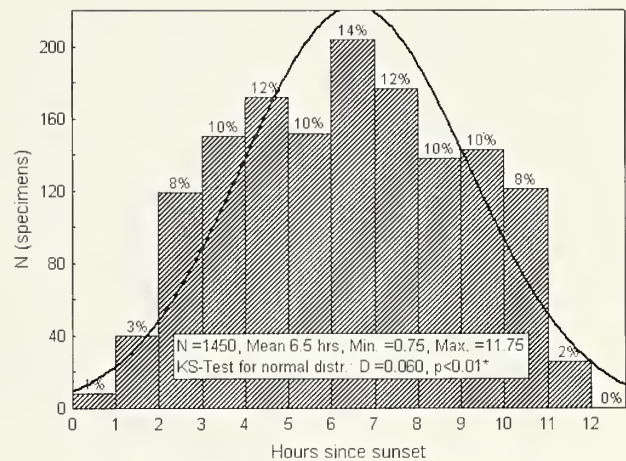


Figure 7: Frequency distribution of arrival times of Sphingidae specimens in Borneo and in Peninsular Malaysia as a function of sampling time. Despite a symmetric distribution around midnight data do not fit a normal distribution.

this reflects the situation at most trapping sites in Southeast-Asia, it might mean that 'physiological' attraction radii are slightly larger than 'ecological', bat-influenced measures of the radii. Weather, moonlight and temperature varied within as well as between sampling nights and might be responsible for a large part of variation in measured attraction radii. All three parameters are known to influence total catch size (e.g. Yela & Holyoak 1997) and might be suspected to influence the flight activity of moths as well as the attraction radii of light sources. Fiedler et al. (pers. com.) found effects of temperature on attraction radii of Geometroidea in temperate Germany, where temperatures vary much more than in tropical lowland areas. However, just like bat predation, such variability only reflects realistic sampling conditions and is therefore not a methodological problem. Whatever physiological differences there might be to influence differences in response to light between species, natural variation in conditions during realistic sampling procedures seems to reduce them to a non-directional 'noise' that will most probably not produce any artifact results in ecological studies.

Completeness of samples

Using the *ChaoI*-estimator (Colwell 2000) as a measure of true species richness, we found that short term (<10 nights), high intensity light trapping (125W MV-lamp, all night hand-sampling) can yield a surpris-

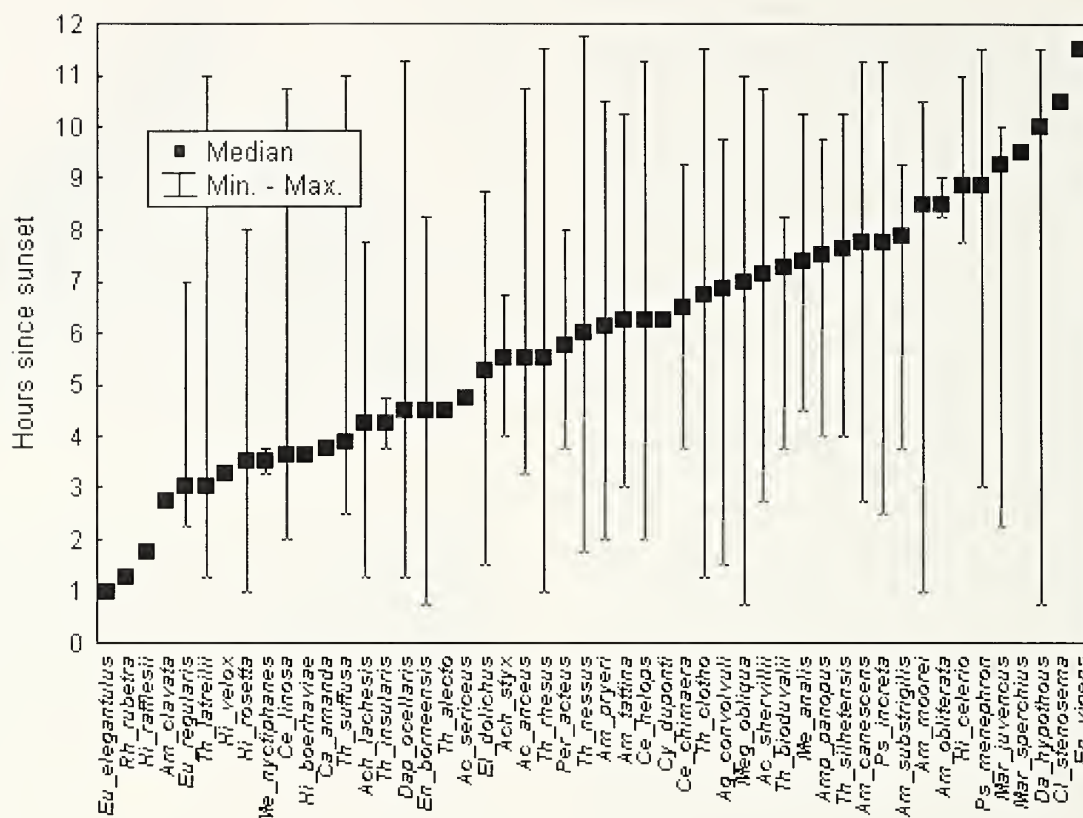


Figure 8: Median, earliest and latest arrival times of 50 Sphingid species in Borneo and Peninsular Malaysia (N=1450). A KW-Anova of the 24 species with individual numbers e"10 indicates that different species have clearly and significantly differing flight times during the night (N=1375, $H_{df=23}=509.04$, $p<0.00001^*$).

ingly complete picture of the species assemblage that is present in a habitat at a particular time (excluding the day-active taxa, of course). An average of $\frac{3}{4}$ of the expected species (and often much more) could be inventoried with this method. Sphingidae are not a very speciose taxon in Southeast-Asia (e.g. species numbers from Borneo: 113 Sphingidae (Beck & Kitching 2004), compared to ca. 1000 described Geometridae (Holloway 1993, 1996, 1997)), but a relatively high degree of available 'background information' even for tropical species (taxonomy, distribution, host plants: Kitching & Cadiou 2000) renders them a very attractive group for ecological research within the Lepidoptera.

It is difficult to judge how reliable species richness estimates really are. *Chao1*-estimates increased with increasing S_{obs} within some sites (see Schulze & Fiedler 2003 for a similar effect on Fisher's α of Pyralidae), even though they often reached relatively stable values with addition of the last 1-2 sample nights (see e.g. figure 5). Alternative estimators (see results) came to very similar figures of expected species, and figure 6 indicates that extrapolation estimates are generally in

a realistic range. Particularly, 'optimal estimators' according to Brose & Martinez (2004) correlate well with *Chao1* (Spearman rank correlation: $N=23$, $R^2=0.525$, $p<0.00001^*$) and lead to an overall very similar assessment of sampling success. Thus, estimates are considered credible, although only more empirical studies on Colwell's (2000) estimators can really judge their value as predictors of true species richness.

Moreno & Halffter (2000) used randomized species accumulation curves to determine asymptotes of species inventories for Neotropical bat assemblages, which were suggested to be used for the comparison of incomplete samples, across different sampling methods or sampling efforts. This was criticized by Willott (2001; but see Moreno & Halffter 2001), who pointed out that (1) the number of sampled individuals is a better measurement of sampling effort than the number of sampling units, and (2) the method is not suitable for high diversity taxa where only a small fraction of a local assemblage has been sampled. The *MMMeans* method of richness estimation (Colwell 2000, Chazdon et al. 1998) follows a

similar approach by fitting an asymptotic Michaelis-Menten type curve to randomized species accumulation curves. *MMMeans*-estimates were generally very similar to *Chao1*-estimates in this study. Figure 5 shows an example of species accumulation curves. Estimates of total species richness from *Chao1* were in an acceptable range when viewing randomized species accumulation curves, which adds credibility to both approaches.

Flight times

The analysis of flight times shows that it is crucial to stay out all night in order to sample Southeast-Asian hawkmoth communities successfully and completely. Not only does the greatest number of specimens come around midnight to the light (and moths keep coming until dawn), but a shorter sampling period would also systematically under-represent certain species, as median flight times vary significantly between species. The ability of Sphingidae to warm up their flight muscles by shivering gives them the ability to make their flight activity relatively independent of ambient temperatures, at least under the moderate temperature changes of a tropical night. However, in other tropical moth taxa empirical data prove that numbers of moths arriving at night decrease after the first few hours (Schulze 2000, Brehm 2002, Süssenbach 2003). Hence, the judgment stated above might not be valid for such taxa, and the 'coverage' of the assemblage in samples may be considerably higher even if sampling is carried out only for parts of the night.

It remains to be seen from similar data on other taxa, if 'niches' in flight time are a general feature of moth assemblages. Anecdotal information points into this direction – Southeast-Asian Saturniidae, for example, are found in numbers only after midnight (pers. obs., see also Janzen 1984). No ecological reasons for temporal niche segregation could be confirmed from our data, though early-flying taxa tended to be smaller than late-flying ones. Studies on other organisms suggest that partitioning of activity times is only rarely caused by competition or predation, and that endogenous rhythmicity may be an evolutionary constraint (e.g. Kronfeld-Schor & Dayan 2003). We did not find any decline in the number of Sphingidae specimens (nor for other groups, though this was not quantified) under conditions of heavy rain. No moths might be flying during the peak minutes of a tropical rainstorm, but they still keep coming under very unpleasant sampling conditions. Thus, breaks from a sampling schedule due to heavy rain (which are commonly reported in the literature) cannot be excused by low sampling success, although more

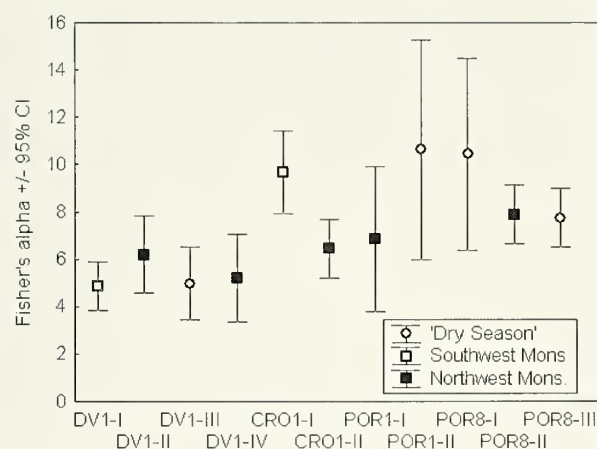


Figure 9: Fisher's α ($\pm 95\%$ confidence interval) as a measure of within-habitat diversity for re-samples of four sites in north-eastern Borneo (see Table 1). Only at one site (CRO1) a significant difference in diversity between re-samples within a site (dashed lines) can be observed. There is no indication for systematic influences of season (see Table 5) on diversity. Fisher's α ($\pm 95\%CI$) for pooled sample sessions are: DV1: 5.98 ± 0.99 , CRO1: 8.15 ± 1.23 , POR1: 8.65 ± 2.46 , POR8: 7.97 ± 1.05 . All samples fit the *logseries*-distribution sufficiently good to justify the use of Fisher's α (Southwood & Henderson 2000).

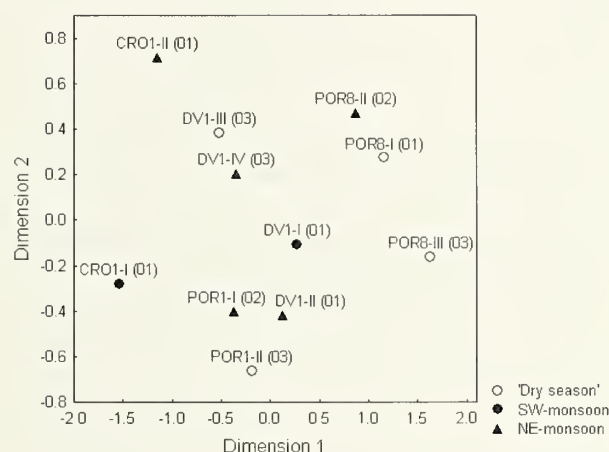


Figure 10: Multidimensional Scaling of *NESS*($m=21$)-values ordinate sampling sessions according to their faunal similarity. Different symbols indicate season (see Table 5 for classification), labels give sample acronyms and the year of sampling (in brackets). Temporal differences (season, year) do not produce meaningful patterns, whereas samples are differentiated according to site affiliation (see text for randomization test).

fragile taxa might be damaged beyond identification by wet equipment.

Table 5. Timing of re-sampling sessions (4-9 nights each) at four sites in Sabah, Borneo. Numbers in brackets indicate 'seasons' based on rainfall measurements at Danum Valley Field Centre (see Marsh & Greer 1992), but our assessment of seasons is based on means of 17 instead of 6 years of meteorological data collection (data not shown, G. Reynolds pers. com.): (1) = 'Dry Seasons' February-April, July-September (<230 mm rainfall per month), (2) = 'South-West Monsoon' May-June, (3) = 'North-East Monsoon' October-January (>250 mm). Climate patterns might differ between parts of Borneo island, see also Walsh & Newbery (1999), Kato et al. (1995), Kitayama et al. (1999).

Site	Sample I	Sample II	Sample III	Sample IV
DV1	Jun 2001 (2)	Dec 2001 (3)	Mar 2003 (1)	Dec 2003 (3)
CRO1	May 2001 (2)	Nov 2001 (3)		
POR1	Jan 2002 (3)	Feb 2003 (1)		
POR8	Jul 2001 (1)	Jan 2002 (3)	Feb 2003 (1)	

Table 6. Measures of between-sample diversity between sampling sessions at four sites in Borneo. All indices range from 0 (no species in common between sessions) to 1 (identical samples). While Sørensen-indices consider only presence-absence data (Southwood & Henderson 2000), NESS-indices (Grassle & Smith 1976) use quantitative data with increasing weight on rare species with increasing m (see e.g. Brehm & Fiedler 2004 for an assessment of between-habitat diversity measures). For comparison between-sample diversity of 10 samples (within 12 months) in seasonal northern Vietnam (Hoang Lien Nature Reserve, data from T. Larsen, pers.com.) is presented.

Site	Re-samples	Sørensen (Mean±SD)	NESS ($m=1$) (Mean±SD)	NESS ($m=21$) (Mean±SD)
DV1	4	0.83 ± 0.18	0.95 ± 0.04	0.85 ± 0.09
CRO1	2	1.00	0.80	0.95
POR1	2	0.67	0.86	0.94
POR8	3	0.87 ± 0.12	0.78 ± 0.07	0.92 ± 0.07
HOA	10	0.47 ± 0.24		

Seasonality and temporal change

We have found no evidence of 'seasonality' in Sphingid assemblages from north-eastern Borneo, though our data were too limited for an application of rigorous tests of cyclic patterns (e.g. Wolda 1988). Previous studies suggested that not only in tropical habitats with clear wet and dry seasons (e.g. Frith & Frith 1985, Janzen 1993), but also in less seasonal regions (Novotny & Basset 1998, Intachat et al. 2001, Wolda 1978) insect abundances can fluctuate considerably as an effect of changes in precipitation. Our data suggests that while there are considerable changes of relative and absolute abundances of individual species between sampling sessions (see below), measures of diversity (figure 9), community structure (Table 6) and the rank order of species (Table 7) are not dramatically different. A number of other studies also concluded that temporal changes did not affect measures of community structure for studies of ants in Borneo (Brühl 2001) or Lepidoptera in Sulawesi (Barlow & Woiwod 1993), New Guinea (Novotny et

al. 2002) and Borneo (e.g. Fiedler & Schulze 2004, Schulze & Fiedler 2003). Thus, in the absence of clear seasonal patterns (see also Walsh & Newbery 1999), we conclude that short-term samples probably give reasonably good data for analyses of local assemblages of Sphingidae in Borneo – even though it has to be kept in mind that assemblages might change over timescales of several years (Beck et al., 2006). For a few species (*Theretra rhesus*, *T. latreillii*, *T. insularis*, *Daphnis hypothous*, *Marumba juvencus*, *Enpinanga borneensis*, *Cechenena lineosa*) we have indications of larger long-term population fluctuations from the re-samples in our data as well as in comparison with older literature (e.g. Holloway 1976, 1987, Tennent 1991).

CONCLUSIONS

From the experimental and empirical data that we presented above, the following conclusions and methodological advice can be drawn:

1) For complete and efficient sampling of Sphingidae (at least in Southeast-Asia), hand-sampling

Table 7: R-values for Spearman rank correlations of relative abundances of species across 11 (re-)sampling sessions in Borneo. All correlations have p-values <0.05* (N=58), values in bold print mark correlations at p<0.0001*. The latter include all within-site correlations of sessions (in boxes).

	DVI-I	DVI-II	DVI-III	DVI-IV	CROI-I	CROI-II	PORI-I	PORI-II	POR8-I	POR8-II
DVI-II	0.812									
DVI-III	0.673	0.624								
DVI-IV	0.650	0.701	0.576							
CROI-I	0.555	0.572	0.465	0.515						
CROI-II	0.493	0.586	0.379	0.410	0.740					
PORI-I	0.603	0.650	0.577	0.525	0.657	0.621				
PORI-II	0.598	0.643	0.504	0.425	0.525	0.549	0.676			
POR8-I	0.359	0.430	0.272	0.274	0.419	0.388	0.309	0.393		
POR8-II	0.425	0.510	0.395	0.409	0.422	0.458	0.538	0.474	0.767	
POR8-III	0.373	0.441	0.370	0.400	0.478	0.449	0.453	0.534	0.775	0.842

at a light source during the whole night is necessary. Shorter nightly sampling sessions miss a considerable number of specimens, and – more importantly – might specifically miss species with particular flight times, which would bias data. However, as long as sampling is kept standardized across habitats to be compared, and provided that the samples are sufficiently large and representative (e.g. by sampling during the peak hours of activity around midnight) between-site comparisons might still yield valid results.

2) Under these conditions, a week of sampling will usually yield over 100 specimens, which often represent more than ¾ of the expected species in a habitat (excluding day-active species). Pre-condition to this is an adequate choice of sampling site, which should sample from some open airspace rather than dense vegetation (Schulze & Fiedler 1997). Seasonality of assemblages can probably be neglected for practical purposes, though care has to be taken when including data from older sources or from more seasonal regions.

3) There is no indication that a significant fraction of specimens are not sampled locally, but drawn from some distant natural habitats to the sampling site by the light. A 125 Watt mercury-vapor bulb has a 50% attraction radius of less than 30 meters (which confirms older measures from the literature), so even highly active, fast-flying taxa such as Sphingidae can be very locally sampled. However, individual specimens might fly far from their normal (breeding) habitat for natural reasons (e.g., dispersal, migration).

4) No evidence was found that species within the family Sphingidae differ significantly in their attraction to light. While this does not generally rule out that such effects may occur, natural variation of sampling conditions will effectively level out such subtle

differences. We tentatively conclude that abundances at light sources do largely reflect relative abundances (or rather flight activity) in a habitat. However, wherever there is an option of comparing relative abundances at light with other measures of relative species abundance (e.g., counts of caterpillars from random samples) these should be employed and critically discussed.

5) There is indication that attraction towards light sources differs between higher taxonomic units such as Lepidopteran families. Large differences in body size or shape might be a key predictor for the dimension of such differences. Data for taxonomically or morphologically diverse assemblages should be critically explored for potential biases resulting from different attraction radii of light. In biodiversity studies that compare different habitats, for example, it should be explored whether different taxonomic sub-units follow similar patterns before they are presented as one common trend from a pooled data set.

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A review of the genus *Manerebia* Staudinger (Lepidoptera: Nymphalidae: Satyrinae) in the northern Andes

TOMASZ W. PYRCZ

Zoological Museum of the Jagiellonian University, Ingardena 6, 30-060 Kraków, Poland
pyrcztomasz@hotmail.com

KEITH R. WILLMOTT

Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA
krwillmott@hotmail.com

JASON P. W. HALL

National Museum of Natural History, Smithsonian Institution, Washington D.C., USA
hallja@si.edu

ANGEL L. VILORIA

Centro de Ecología, Instituto Venezolano de Investigaciones Científicas, Apartado 21827, Caracas 1020-A, Venezuela
aviloria@oikos.iivic.ve

Abstract: The taxonomic limits of the neotropical montane satyrine genus *Manerebia* Staudinger are defined, with the names *Penrosada* Brown and *Posteuptychia* Forster treated as junior subjective synonyms. The taxonomic history of the genus is discussed and the current knowledge on the distribution, ecology and behavior of all north Andean species is summarised. A species-level taxonomic review of north Andean *Manerebia* is presented that includes 23 species and 37 taxa. Of these, 10 new species and 13 new subspecies are described here: *M. germaniae* n. sp., *M. golondrina* n. sp., *M. magnifica* n. sp., *M. mammothus* n. sp., *M. pervaga* n. sp., *M. pluviosa* n. sp., *M. prattorum* n. sp., *M. rufanalis* n. sp., *M. seducta* n. sp., *M. undulata* n. sp., *M. franciscae rodriguezi* n. ssp., *M. germaniae vitalei* n. ssp., *M. inderena antioquiensis* n. ssp., *M. inderena clara* n. ssp., *M. inderena fina* n. ssp., *M. inderena leaeniva* n. ssp., *M. inderena mirena* n. ssp., *M. inderena similis* n. ssp., *M. leaena gonzalezi* n. ssp., *M. rufanalis fernandina* n. ssp., *M. satura lamasi* n. ssp., *M. satura pauperata* n. ssp., *M. undulata milaena* n. ssp. A lectotype is designated for *M. leaena* to stabilise future nomenclature and *Penrosada lanassa* f. *neglecta* is placed as a subspecies of *Manerebia ignilimeata* n. stat. Accounts are presented for each species, discussing identification, taxonomy and ecology, and listing known geographic and elevational range data. Adult specimens, drawings of male genitalia and distribution maps are figured for all taxa where possible and the location of type material is given.

Key Words: cloud forest, Colombia, ecotone, Ecuador, elevational range, elfin forest, identification, *M. franciscae rodriguezi* n. ssp., *M. germaniae* n. sp., *M. germaniae vitalei* n. ssp., *M. golondrina* n. sp., *M. inderena antioquiensis* n. ssp., *M. inderena clara* n. ssp., *M. inderena fina* n. ssp., *M. inderena leaeniva* n. ssp., *M. inderena mirena* n. ssp., *M. inderena similis* n. ssp., *M. seducta* n. sp., *M. leaena gonzalezi* n. ssp., *M. magnifica* n. sp., *M. mammothus* n. sp., *M. pervaga* n. sp., *M. pluviosa* n. sp., *M. prattorum* n. sp., *M. rufanalis* n. sp., *M. rufanalis fernandina* n. ssp., *M. satura lamasi* n. ssp., *M. satura pauperata* n. ssp., *M. undulata* n. sp., *M. undulata milaena* n. ssp., páramo, *Penrosada*, Peru, *Posteuptychia*, systematics, taxonomy, tree-line, Venezuela.

INTRODUCTION AND METHODS

The taxonomy of the neotropical Satyrinae remains the most poorly understood of any nymphalid butterfly group. The high levels of endemism and diversity in the tropical Andes make understanding the systematics of its fauna particularly challenging,

and this is certainly true of the speciose genus *Manerebia* Staudinger. A notable feature of the genus is the external similarity of many species, which can only be identified with certainty through dissection, and this fact has led to much confusion in the literature and resulted in a significant underestimation of the true taxonomic diversity of the genus. In this paper we review the *Manerebia* fauna of the north Andean region, where the highest number of undescribed and taxonomically confusing taxa occur. The genus is

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remarkable for only 13 of the 23 known north Andean species, and 14 of the 37 known north Andean taxa, having been described to date, clearly illustrating the importance of continuing collection activity in this region. We aim to establish the identity of all historical names applying to taxa from this region and describe all unnamed taxa known to us, hopefully creating a firm foundation for future taxonomic revision of the entire genus.

The authors have been involved in studying the diversity and taxonomy of the Andean satyrine butterflies of Venezuela, Colombia and Ecuador for more than a decade (e.g. Pyrcz *et al.*, 1999; Pyrcz & Vilorio, 2004; Vilorio, 2001). The region between southern Ecuador and northern Peru forms a prominent biogeographic divide for many montane butterfly taxa (Willmott, Hall, Pyrcz, unpublished data), and the majority of north Andean *Manerebia* species do not occur further to the south. We therefore define, for the purpose of this paper, the north Andes as the area north of the Río Chamaya - Marañón valley in northern Peru, also known as the Huancabamba deflection (Dillon, 1994).

Original descriptions were consulted for all published *Manerebia* names and attempts made to locate type material. *Manerebia* specimens were examined in collections in Europe, North and South America, as listed below. One problem faced by earlier authors was a lack of reliably labelled material in collections. However, extensive fieldwork throughout the region by ourselves and others has provided a large amount of new information on habitat preferences, geographic and elevational distribution and phenotypic variation. This information has been extensively used in proposing new relationships between allopatric taxa, but we have nevertheless had to make a number of arbitrary assignments of taxonomic rank, based on incomplete information. In general, where there are no apparent differences in either genitalic characters, or wing pattern characters that do not vary intraspecifically elsewhere in the genus, and closely allopatric taxa have similar elevational ranges and occur in similar habitats, we have regarded them as conspecific.

Dissections were made of males only, due to the rarity of females in collections, and where necessary, type specimens were dissected to confirm their identity. Abdomens were soaked in hot 10% KOH solution for 15 min and subsequently stored in glycerol for study under binocular microscope. Morphological terms for genitalia largely follow Klotz (1956) and for venation follow Comstock & Needham (1918). The following collection codens are used in the text:

AFEN: Collection of Andrew F. E. Neild, London, UK
AME: Allyn Museum of Entomology, Sarasota, USA (now at

McGuire Center for Lepidoptera and Biodiversity, Gainesville, USA)

BMNH: The Natural History Museum, London, UK (T=Type coll., R=Rothschild coll., A&B=Adams & Bernard coll.)

GR: Collection of Gabriel Rodríguez, Medellín, Colombia

IMLT: Fundación e Instituto Miguel Lillo, Tucumán, Argentina

JFLC: Collection of Jean-François Le Crom, Bogotá, Colombia

KWJH: Collection of Keith Willmott and Jason Hall, Gainesville, USA

MALUZ: Museo de Artrópodos de la Universidad del Zulia, Maracaibo, Venezuela

MBLI: Collection of Maurizio Bollino, Lecce, Italy

MECN: Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador

MHNUN: Museo de Historia Natural de la Universidad Nacional, Bogotá, Colombia

MHNUP: Museo de Historia Natural de la Universidad Pedagógica, Bogotá, Colombia

MIZA: Museo de Entomología de la Universidad Central, Maracay, Venezuela

MZPAN: Muzeum i Instytut Zoologii Polskiej Akademii Nauk, Warsaw, Poland

MUSM: Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru

MZUJ: Muzeum Zoologiczne Uniwersytetu Jagiellońskiego, Kraków, Poland.

PB: Collection of Pierre Boyer, Le Puy Sainte Réparate, France

PUCE: Museo de Entomología, Pontificia Universidad Católica del Ecuador, Quito

PUJ: Departamento de Biología, Pontificia Universidad Javeriana, Bogotá, Colombia

SMTD: Staatliche Museum für Tierkunde, Dresden, Germany

TWP: Collection of Tomasz Wilhelm Pyrcz, Warsaw, Poland

USNM: United States National Museum - Smithsonian Institution, Washington, USA

ZMHU: Museum für Naturkunde der Humboldt Universität, Berlin, Germany

DHW, VHW, DFW, VFW: dorsal hindwing, ventral hindwing, dorsal forewing, ventral forewing

Systematic overview

The name *Manerebia* was initially proposed by Staudinger (1897) for five new, closely related Bolivian and Peruvian species (*M. cyclopina*, *M. cyclopella*, *M. cyclops*, *M. typhlops* and *M. thyphlopsella*). Subsequent taxa described in the genus were also typically from the southern tropical Andes (Schaus, 1902; Hayward, 1949; Forster, 1964), with the exception of the Colombian *M. nevadensis* Krüger (Krüger, 1925) and Ecuadorian *M. keradialeuka* Hayward (Hayward, 1968). Brown (1944) introduced the generic name *Penrosada* for a cluster of mainly north Andean species formerly often placed in *Lymanopoda* Westwood, 1851, including *P. leaena* (Hewitson), *P. apiculata* (C. & R. Felder), *P. lanassa* (C. & R. Felder), *P. lisa* (Weymer, 1911), *P. satura* (Weymer), *P. cillutinarca* (Weymer, 1912, a synonym of *M. zoippus* (H. Druce, 1876)), and *P. keithi* (Dyar, 1913, a synonym of *M. satura*). Adams & Bernard (1979, 1981) and Adams (1986) described a further four species of *Penrosada* from Colombia and Venezuela, and historically authors have continued

to regard both *Manerebia* and *Penrosada* as distinct genera, without further discussion of the taxonomic relationships of their members (e.g., Forster, 1964; Miller, 1968; Adams & Bernard, 1977, 1979, 1981; Adams, 1985, 1986; D'Abbrera, 1988; Racheli & Racheli, 2001).

Having examined the head, thorax, wing venation and pattern, and male genitalia of all species formerly placed in *Penrosada* Brown and *Manerebia* we have found no synapomorphies that distinguish the two genera, and we therefore follow Lamas & Vitoria (2004) in considering the former as a subjective junior synonym of the latter. Brown's (1944) original description of *Penrosada* made no reference to *Manerebia*, and his morphological diagnosis of the genus applies fully to the species originally treated in *Manerebia* by Staudinger (1897), namely, the hindwing vein M1-M2 is characteristically short (shorter than in *Lymanopoda* Westwood) and gently curved, the root of vein M3 is much closer to vein Cu1 than M2, the hindwing is slightly incised near the anal angle, the ocellus in cell 1A-Cu2 of the forewing and hindwing is usually fully developed, and the walking legs are yellowish. The conspicuous oblique, straight yellow or whitish band on the hindwing underside present in most *Penrosada* of Brown and absent in the five original *Manerebia* of Staudinger almost certainly does not define a monophyletic group, being highly variable between and even within populations. Some species of *Manerebia*, as defined here, such as *M. ignilineata*, *M. interrupta* and *M. apiculata*, are polymorphic, with the band shortened, discontinuous or even entirely absent. Other typical features of the genus *Manerebia* include male genitalia characterised by a long, arched uncus, fully developed subuncus, and slender valvae with a strongly dentate dorsal edge.

We also consider the genus *Posteuptychia* Forster a subjective junior synonym of *Manerebia*, where it was placed by Lamas & Vitoria (2004). Forster (1964) erected the monotypic *Posteuptychia* for *Pronophila mycalesoides* C. & R. Felder on the strength of its slightly unusual male genitalic morphology, but did not notice that species he treated in *Manerebia* were also similar in this respect, and shared similar wing color pattern and venation. Indeed, *M. mycalesoides* is perhaps genitally most similar to *M. nevadensis*, one of the few north Andean species actually originally described in *Manerebia*.

Miller (1968) placed *Manerebia* in the tribe Pronophilini Reuter, a neotropical section of the Satyrinae. Adams & Bernard (1977, 1979, 1981), Adams (1986) and Pyrcz (1999) did not question this decision, but Vitoria (2001) suggested that *Manerebia* does not belong in the Pronophilina, but in the pre-

dominantly Holarctic Erebiina (following Harvey's (1991) arrangement, downranking former tribes to subtribes of the Satyrini). Vitoria (2001) listed three putative synapomorphies of the Pronophilina absent in *Manerebia*: setose eyes, hindwing cross vein M1-M2 curved basad into the discal cell and hindwing discal cell equal or shorter than the maximum length of the hindwing. The absence of setae on the eyes also occurs in the Erebiina, where the genus is currently placed (Lamas & Vitoria, 2004), as well as in the Palearctic Satyrina. We believe the character evidence in support of this subtribal position is currently weak, and a thorough cladistic analysis of the tribe Satyrini is clearly needed, hopefully including additional characters, especially those from the early stages (e.g., Harvey, 1991) and molecular sequence data. Pyrcz (1995) and Vitoria (2001) suggest *Tamania* Pyrcz or *Idioneurula* Strand as possible sister genera of *Manerebia*.

The species-level systematics of *Manerebia* are very complex and have not been rendered easier by multiple errors made by earlier workers (see Appendix 1). Three publications are especially significant for the description of new taxa: Brown (1944), Forster (1964) and Adams (1986). In addition to describing the generic synonym *Penrosada*, Brown (1944) also attempted to treat all Ecuadorian species, though he seemed unaware of two species already described at that time from the country, *M. trimaculata* and *M. ignilineata*, redescribing the latter as forms of "*Penrosada lanassa*". He also mistakenly applied the names *leana*, *lanassa* and *apiculata* to various species and described several infrasubspecific forms differing in the expression of the hindwing band as new taxa. In the absence of any figures of specimens, identification of the taxa that Brown was really treating must be based largely on the imprecise genitalic illustrations. Forster (1964) clarified, to some extent, the classification of the Bolivian species and illustrated the most poorly known taxa described by Staudinger (1897). Unfortunately, he did not examine the genitalia of any species, and hence he also did not notice that *Penrosada* and *Posteuptychia* were morphologically similar to other *Manerebia*. Finally, Adams (1986) treated most of the species of *Manerebia* (under the name *Penrosada*) occurring in Colombia and Venezuela, providing valuable distributional data and describing a number of new taxa, but also made some errors in identification similar to earlier authors. Lamas & Vitoria (2004) provided a synonymic checklist for the entire genus, thus correcting previous taxonomic errors.

Morphology

The wing patterns of all *Manerebia* species are very

simple (Figs. 1-9). Both dorsal and ventral surfaces are generally uniformly brown (though *M. lisa* and two new species described here have a coloured dorsal band), and the most visible character, the ventral hindwing postdiscal band, is also one of the most variable. In addition to simple local and geographic variation in width, orientation and color, the band may be absent altogether, split into spots, or reduced to small sections, all within a single population. The evolutionary basis for the polymorphism within this hindwing band remains unknown, but it occurs in several species that are apparently not a monophyletic group. The only other apparent pattern elements are fine, darker postdiscal and submarginal lines, and occasional submarginal ocelli in cells Cu1-Cu2 on the forewing and cells Cu1-Cu2 and 1A-Cu2 on the hindwing, and these subtle characters prove to be some of the most useful for distinguishing species.

The male genitalia (Figs. 10-14) are also taxonomically extremely useful, for although also simple in structure they may differ significantly between species that are externally almost indistinguishable. In the north Andean fauna, taxa frequently fall into one of two principal morphological groups (that may or may not be monophyletic); one in which the uncus is strongly arched, the subunci relatively long, the 'teeth' at the distal tip of the valva often extending anteriorly along the dorsal edge, and the dorsal base of the valva armed with a projection with numerous small 'teeth' (*M. leana*, *M. germaniae*, *M. pluviosa* n. sp., *M. apiculata*, *M. navarrae*, *M. franciscae*, *M. mammothus* n. sp., *M. satura*), and one in which the uncus is slightly curving or straight, the subunci relatively short, the 'teeth' confined to the distal tip of the valva, and the dorsal base of the valva armed with a simple projection only (*M. inderena*, *M. golondrina* n. sp., *M. prattorum* n. sp., *M. trimaculata*, *M. undulata* n. sp., *M. interrupta*). Within these two groups, more subtle characters in the shape of the uncus, subunci and valvae are often consistent within and between populations, and provide clues to the relationships of allopatric taxa.

Diversity, distribution, ecology and behavior

Lamas & Vilorio (2004) recognise a total of 45 *Manerebia* species, including both described and undescribed species. The genus is exclusively Andean, including the peripheral ranges of Sierra Nevada de Santa Marta and the Venezuelan Cordillera de la Costa (Figs. 15-20), and local faunas in the central and northern Andes comprise three to eight species (Appendices 2, 3). Some species of *Manerebia* occur in premontane forests as low as 800 m (*M. mycalesoides*, *M.*

magnifica n. sp. and some Bolivian species). The genus is, however, most diverse in middle and upper elevation cloud forest and elfin forests from 2300-3000m. A few species occur in the páramo grassland above the tree line up to 4000m (*M. levana*, *M. ignilineata*, *M. seducta* n. sp.).

Most north Andean *Manerebia* occur in low population densities. This is particularly true for species in Venezuela and northern Colombia, where they are among the rarest cloud forest butterflies. *Manerebia mycalesoides*, the sole representative of the genus in the Venezuelan Cordillera de la Costa, remained unknown there until 1999, despite this being probably the best sampled mountainous area in South America. In Colombia and Ecuador *Manerebia* species abundance remains relatively low in comparison to that of other sympatric cloud forest satyrine genera, such as *Pedaliodes* Butler, 1867, *Pronophila* Doubleday, [1849], or *Lymanopoda*. Aggregations at water seepages of more than a couple of individuals are a rare sight, but, surprisingly, towards the southern tropical Andes the reverse may be true. In the cloud forests of Bolivia certain species of *Manerebia* are occasionally extremely abundant, and literally hundreds of individuals can be frequently observed along roadsides and forest trails (Pyrz, pers. obs.). Seasonal fluctuations in abundance have also been noted (Adams & Bernard, 1981) for some north Andean species, especially those occurring in the páramo. Adults of some species are observed almost exclusively during the wet season (*M. franciscae*, *M. interrupta*), whereas others seem to be much more abundant during the dry season (*M. undulata* n. sp., *M. inderena*).

Several *Manerebia* species are confined to very narrow ecological zones, such as the forest-páramo ecotone (*M. interrupta*), while other north Andean *Manerebia*, although wider ranging, are inconspicuous butterflies of dense cloud forests, usually overlooked by lepidopterists. These facts have resulted in their poor representation in major collections. Fortunately, however, all of the cloud forest species of *Manerebia* are readily attracted to decomposing organic matter, especially dung and carrion, and the use of baited traps provides a rapid and reliable method of sampling. Páramo species also come to bait, but less readily, and sampling for species above the tree-line must also be done with hand-nets.

Some species of *Manerebia* demonstrate notable wing pattern similarities to unrelated, microsympatric pronophiline satyrines. Adams & Bernard (1979) remarked on the similarity of two Colombian species, *M. quinterae* and *M. navarrae*, to two respectively sympatric *Eretris* species, and stated that there was "little doubt" that mimicry was occurring. A further, even

more striking example concerns *M. pluviosa* n. sp., which has a very unusual wing pattern for the genus, a wide postdiscal orange band on both wings. This species is microsympatric with a similarly patterned *Pedaliodes* species (Pyrce & Vitoria, in press). To date there is no evidence for unpalatability in any of these species, and it remains to be demonstrated that these similarities result from mimicry.

Very little is known about the early stages of *Manerebia*. Adams & Bernard (1981) recorded the montane bamboo *Chusquea* (Poaceae) as the food plant for *Manerebia franciscæ*. Greeney (Greeney & Pyrcz, in prep.) observed second to fourth instar larvae of *M. inderena clara* n. ssp. in Yanayacu (Ecuador, Napo) also on a species of *Chusquea*. This food plant is also that of most Neotropical cloud-forest satyrines and will probably apply to the entire genus.

SPECIES ACCOUNTS

Manerebia Staudinger, 1897

Manerebia Staudinger, 1897: 139. Type-species *Manerebia cyclopi-na* Staudinger, by subsequent designation (Hemming, 1943: 24).

= *Penrosada* Brown, 1944: 255. Type-species *Lymanopoda leaena* Hewitson, by original designation.

= *Posteuptychia* Forster, 1964: 137. Type-species *Pronophila mycalesoides* C. & R. Felder, by monotypy.

[NOTE: only north Andean taxa are included here, with the exception of *M. satura satura*; - indicates a subspecies, — indicates a synonym]

leaena (Hewitson, 1861)

-*lanassa* (C. & R. Felder, 1867)

-*gonzalezi* Pyrcz & Vitoria, n. ssp.

-*germaniae* Pyrcz & Hall, n. sp.

-*vitalei* Pyrcz & Willmott, n. ssp.

-*pluviosa* Pyrcz & Vitoria, n. sp.

-*apiculata* (C. & R. Felder, 1867)

—*curvilinea* Weymer, 1912

-*franciscæ* (Adams & Bernard, 1981)

-*rodriguezi* Pyrcz & Willmott, n. ssp.

-*mammuthus* Pyrcz & Willmott, n. sp.

-*satura* (Weymer, 1911)

-*pauperata* Pyrcz & Willmott, n. ssp.

-*lamasi* Pyrcz & Willmott, n. ssp.

-*navarrae* (Adams & Bernard, 1979)

-*quinterae* (Adams & Bernard, 1979)

-*inderena* (Adams, 1986)

-*antioquiensis* Pyrcz & Willmott, n. ssp.

-*fini* Pyrcz & Willmott, n. ssp.

-*similis* Pyrcz & Willmott, n. ssp.

-*clara* Pyrcz & Willmott, n. ssp.

-*leavenia* Pyrcz & Willmott, n. ssp.

-*mirena* Pyrcz & Willmott, n. ssp.

-*golondrina* Pyrcz & Willmott, n. sp.

-*prattorum* Pyrcz & Willmott, n. sp.

-*trimaculata* (Hewitson, 1870)

-*undulata* Pyrcz & Hall, n. sp.

-*milaena* Pyrcz & Willmott, n. ssp.

-*interrupta* (Brown, 1944)

—*keradialeuka* (Hayward, 1968)

-*rufanalis* Pyrcz & Hall, n. sp.

-*fernandina* Pyrcz & Willmott, n. ssp.

-*ignilineata* (Dognin, 1896)

-*neglecta* (Brown, 1944) n. stat.

—*discontinua* (Brown, 1944)

-*seducta* Pyrcz & Willmott, n. sp.

-*mycalesoides* (C. & R. Felder, 1867)

—*lethe* (Butler, 1867)

-*magnifica* Pyrcz & Willmott, n. sp.

-*nevadensis* Krüger, 1925

-*levana* (Godman, 1905)

-*pervaga* Pyrcz & Vitoria, n. sp.

Manerebia leaena (Hewitson, 1861)

The identity of *leaena*, the oldest available name in *Manerebia*, is crucial for establishing a stable nomenclature for this genus in the northern Andes. The original description is concise ("Upperside dark brown from the base to the middle, rufous-brown [beyond. Underside as above, except that the posterior wing is crossed transversely beyond the middle, from margin to margin, by a regular, nearly straight band of pale yellow. Exp. 19/20 inch") and accompanied by a black and white figure of the ventral surface (Hewitson, 1861). Hewitson did not give any type locality, sex or number of specimens examined, which makes the correct identification of *leaena* difficult. However, several other pronophiline satyrines were described in the same paper (e.g., *Lymanopoda lactea*, *Lymanopoda labda*, *Lymanopoda albocincta*), all of which were from Colombia.

Kirby (1879), in his catalogue of butterflies in the collection of Hewitson in the BMNH, mentions seven specimens of *leaena* from Ecuador. Four Hewitson specimens labelled as *leaena* were located at the BMNH, including two labelled Ecuador and two without any locality. Since these specimens actually represent two different species, *M. leaena* and *M. undulata* n. sp., a lectotype designation is necessary. The specimen selected as the lectotype of *leaena* very closely matches the original figure, in particular in the precise shape of the pale hindwing ventral surface band, which is slightly notched along the basal edge at the base of vein M3 and tapers at the tornus, and in its uniform ground colour and lack of ocelli. Given the accuracy of Hewitson figures, we believe it is probably the specimen on which the illustration was based. The specimen has a typed label, which would have been added subsequent to the specimen's accession to the BMNH, which has "?Ecuador" written on it, with "Quito" written over the top. Presumably the original specimen lacked locality data and a guess was made as to its origin based on other similar Hewitson specimens. However, a very careful comparison of *leaena*-like specimens from all sampled localities in Ecuador

(specified in this paper) and Colombia reveals that the wing shape and colour pattern of the lectotype matches perfectly only those found in the Colombian Cordillera Oriental east of Bogotá. Adams (1986) collected a series of specimens of *M. leaena* recently in that area. The genitalia of the lectotype confirm this, being typical of Colombian *leaena* as treated here. It is not the only case when a pronophiline butterfly described by Hewitson bears incorrect "Ecuador" locality data. *Eretris phyllalia* (Hewitson), whose syntype specimen shares the same type of label as the lectotype of *leaena*, is a synonym of *Eretris apuleja apuleja* (C. & R. Felder, 1867) found in the vicinity of Bogotá.

Having no access to the British type material, Brown (1944) misidentified *M. leaena* and applied the name to an uncertain number of Ecuadorian species. Adams (1986) correctly recognised that *M. leaena* is found in the Bogotá region, but implied that it was sympatric with *M. l. lanassa*, which he considered a separate species. He treated *M. leaena* as a species occurring throughout the eastern Andes from Colombia to Peru, and figured the genitalia of a Peruvian specimen of *Manerebia haywardi* (Pyrz, 2004) that is similar externally but actually has very distinct genitalia. Hence, the genitalia illustrations of *M. leaena* and most other taxa in Brown (1944) and Adams (1986) are incorrect. Further misidentifications are found in D'Abrera (1988), whose treatment was based on the arrangement of the main collections in the BMNH, and corrections to names of figured specimens are provided here (Appendix 1). In fact, *M. leaena*, although externally similar to many other species, has distinctive male genitalia, which have a toothed projection near the base of the ampulla and a strongly arched uncus, similar to *M. germaniae* n. sp., *M. pluviosa* n. sp., *M. apiculata*, *M. navarrae*, *M. satura*, *M. franciscæ* and *M. mammuthus* n. sp. Within this group, the short, squat valvae, with numerous spines at the tip and pronounced spines on the ampulla, closely resemble only those of *M. germaniae* n. sp. However, *M. leaena* consistently differs from *M. germaniae* in having fewer spines on the dorsal edge of the valva near the base. In addition, the thin dark brown submarginal lines on the ventral surface are undulate in *M. leaena*, but almost straight in *M. germaniae*. Although these two taxa are not known to be sympatric to date, the wing pattern and genitalic characters that distinguish them are consistent throughout their respective ranges (with the exception of a single specimen of *M. leaena leaena* discussed under that taxon). In addition, *M. germaniae* may actually prove to be the sister taxon of *M. pluviosa* (see under that species), which also has straight ventral submarginal lines, and which occurs sympatrically with *M. leaena*

gonzalezi n. ssp. in the Venezuelan Sierra de El Tamá. There is slight subspecific genitalic variation in *M. leaena*, in the number and distribution of spines along the dorsal edge of the valva.

Manerebia leaena leaena (Hewitson, 1861)

Figs. 1A,B, 10A, 15

Lymanopoda leaena Hewitson (1861: 156, pl. 9, fig. 1). **TL:** [Colombia, Cordillera Oriental]. **LT male** (here designated): "Ecuador, Quito", Hewitson Coll. 79-69. B.M. Type No. Rh. 3935. BMNH(T) [examined].

Penosada leaena (Hewitson); Brown (1944: 256) (misidentification).

Manerebia leaena (Hewitson); Lamas & Vilorio (2004: 215).

Diagnosis: In the nominate subspecies (Figs. 1A, B) the VHW postdiscal band is approximately twice the width of that in *M. leaena lanassa*, and also broader than in *M. l. gonzalezi* (described below). This taxon is similar in wing pattern to *M. inderena leaeniva* (described below), but the VHW band is slightly contracted basally at the anal margin and a richer yellow than in *M. inderena leaeniva* or *M. inderena clara* (described below). In addition to the characters given in the species account above, *M. germaniae* n. sp. is also generally larger, has narrower VHW postdiscal bands and a characteristic convex FW outer margin, that is straight in *M. leaena*. A single male specimen in the BMNH(A&B) from the Colombian Sierra Nevada del Cocuy has straighter ventral submarginal lines, similar to *M. germaniae*, but the genitalia, size and other wing pattern characters suggest that it is a slightly aberrant specimen of *M. leaena*.

Comments: The nominate subspecies occurs in the Cordillera Oriental in Colombia (Cundinamarca, Boyacá) on the eastern slopes of the Andes, in Gachetá at 2500 m (Adams, 1986) and Cruz Verde, over 2700m (Krüger, 1925). Remaining literature localities must be considered less reliable, with some probably applying to *M. inderena* (Adams, 1986). Pyrcz's (1999) report of a specimen of *M. leaena* collected by Krüger in the Cordillera Central refers to *M. germaniae* n. sp. (described below).

Manerebia leaena lanassa (C. & R. Felder, 1867), **stat. rest.**

Figs. 1C, D, 10B, 15

Pronophila leaena var. *lanassa* C. & R. Felder (1867: 474). **TL:** Colombia, Cundinamarca, Bogotá. **HT male:** Colombia, Cundinamarca, Bogotá, Lindig, Felder coll. BMNH(R) [examined].

Lymanopoda leaena form *lanassa* (C. & R. Felder); Weymer (1911: pl. 52, row f; 1912: 249).

Penosada lanassa (C. & R. Felder); Brown (1944: 258) (misidentified); Adams (1986: 305).

Manerebia leaena lanassa (C. & R. Felder); Lamas & Vilorio (2004: 215).

Diagnosis: Male genitalic and wing pattern characters show that this taxon is very closely related to *M. leaena leaena*. The male genitalia (Fig. 10B), including that of the holotype, share the characters of other *M. leaena* subspecies, an arched uncus and spines at the dorsal edge of the valva near the base. However, the latter are less prominent, there are no 'teeth' between the shoulder and the apex, the apical 'teeth' are fewer and the valva is more slender. The VHW yellow band is half the width of nominate *M. leaena* and slightly narrower than in *M. l. gonzalezi* n. ssp. Adams (1986) considered *M. leaena* and *lanassa* to be separate species, and stated that the latter taxon occurred on both slopes of the Colombian Cordillera Oriental. However, we have found no evidence to support the latter statement, and a careful examination of Adams material deposited in the BMNH, and material in collections in Bogotá did not reveal any specimen of *lanassa* from the east slopes of the Cordillera. Similarly, in other consulted collections (TWP, JFLC, MHNUP,

PUJ) this taxon is represented only by specimens collected west and northwest of Bogotá. Since *lanassa* therefore seems to be the western slope replacement of *M. leaena leaena*, we consider the two taxa conspecific (Lamas & Vilorio, 2004).

Comments: *Manerebia leaena lanassa* is restricted to the western slope of the Cordillera Oriental in Colombia (Cundinamarca, Boyacá). Adams (1986) reports that it occurs from 2250-2700 m, while TWP has collected it at 2900 m near Facatativá.

***Manerebia leaena gonzalezi* Pyrcz & Vilorio, n. ssp.**

Figs. 1E, 10C, 15

Manerebia leaena n. ssp. (Pyrcz & Vilorio); Lamas & Vilorio (2004: 215).

Diagnosis: This taxon differs from the nominate subspecies primarily by having narrower VHW postdiscal bands, that are, however, not as narrow as in *M. leaena lanassa*. The VHW postdiscal band is slightly arched in comparison with the straighter bands of *M. l. lanassa* or the nominate subspecies. The genitalia (Fig. 10C) are also distinct in having additional 'teeth' along the whole dorsal edge of the valva.

Description: MALE (Fig. 1E): *Head, thorax* and *abdomen*: same as in other subspecies. *Wings:* Forewing (length: 18.5-19 mm, mean: 18.75 mm, n = 4) triangular, tornus obtuse. Hindwing rounded, anal margin very slightly excavated near angle. DFW uniform coffee brown. DHW coffee brown; reddish scales sparsely scattered towards submarginal and marginal areas; basal half of hindwing with dense, long hairs. VFW dark brown; reddish scales scattered along costal margin and distal half of wing, more heavily towards apex and marginal area; submarginal dark chocolate brown zigzag line; vestigial postdiscal white dot in cell Cu1. VHW ground colour chestnut, except for veins which are covered with chocolate brown scales; narrow yellow band (c. 1 mm wide) from apex to anal margin close to tornal angle, crossing just at extremity of discal cell but not entering into it, dark brown submarginal line lightly undulate. *Male genitalia* (Fig. 10C): similar to other subspecies except with additional 'teeth' along dorsal edge of valva.

FEMALE: Unknown.

Etymology: We dedicate this new subspecies to Luis Alfonso González, a forest guard of the Venezuelan Parque Nacional El Tamá, one of the few in the area who knows every detail of its geography and nature, in gratitude for his cooperation and hospitality.

Types: *Holotype male:* VENEZUELA: Táchira, Parque Nacional El Tamá, selva nublada arriba de Betania, 2400-2480 m, 24.VIII.1996, A. Vilorio leg., MALUZ; *Paratypes (3 males):* VENEZUELA: **1 male:** Táchira, Parque Nacional El Tamá, vía La Línea, 2300-2700 m, 17.IV.1996, T. Pyrcz leg., TWP; **1 male:** Táchira, vía Bramón a Delicias, Mata Mula, 1850-2020 m, 18.IX.1997, A. Neild leg., AFEN; COLOMBIA: **1 male:** Norte de Santander, Parque Nacional Natural El Tamá, Herrán, 2500 m, XII.1993, J. F. Le Crom leg., JFLC.

Comments: *Manerebia leaena gonzalezi* is known from a few individuals seen and collected in the cloud forest at elevations between 2300-2700 m. It flies high around bamboos (*Chusquea*) along with *Lymanopoda lebbaea* C. & R. Felder, 1867, ssp. (Pyrcz & Vilorio, in press), *Lymanopoda albocincta* (Hewitson, 1861) and *Eretris porphyria* (C. & R. Felder, 1867) ssp. (Pyrcz & Vilorio, in press), but it is not such a fast flying insect as most of the butterflies found with it.

***Manerebia germaniae* Pyrcz & Hall, n. sp.**

This species is superficially very similar to several sympatric *Manerebia*, especially *M. inderena*. *Manerebia inderena* is best distinguished by the usual presence of submarginal ocelli on the VHW that are most visible in cells Cu2-Cu1 and Cu1-M3, while in *M. germaniae* the pale dots representing the submarginal ocelli

are most visible in the middle of the wing. Also, in most *M. inderena* taxa the thin dark submarginal line is undulate, but straighter in *M. germaniae*. The male genitalia of *M. germaniae*, however, which has a toothed projection near the base of the ampulla and strongly arched uncus, readily helps distinguish *M. germaniae* from all other externally similar species. The genitalia is most similar to that of *M. leaena*, *M. pluviosa* n. sp., *M. apiculata*, *M. navarrae* and *M. saluta*. Within this group, the short, squat valvae, with numerous spines at the tip and pronounced spines on the ampulla, are most similar to probable close relatives *M. leaena* and *M. pluviosa*, both of which also occupy similar habitats and occur allopatrically. In comparison with *M. leaena*, *M. germaniae* has more 'teeth' at the dorsal edge of the valva, is larger, and the submarginal lines on the ventral surface are nearly straight (rather than zigzag), running close to the outer margin. The latter character also occurs in *M. pluviosa*, which is easily distinguished by wing pattern and which is sympatric with *M. leaena* in the Venezuelan Sierra de El Tamá.

There is considerable infraspecific variation in *M. germaniae* involving the width of the VHW yellow postdiscal band, but only one geographic population is differentiated enough to deserve subspecific status. However, when additional data become available, more fine-scale patterns in geographic variation in *M. germaniae* may become apparent.

***Manerebia germaniae germaniae* Pyrcz & Hall, (n. sp.)**

Figs. 1E,G, 10D, 15

Manerebia n. sp. (Pyrcz, Willmott & Hall); Lamas & Vilorio (2004: 216, n. 1123).

Diagnosis: The nominate subspecies differs from *M. g. vitalei* in having a narrower yellow postdiscal band on the VHW.

Description: MALE (Fig. 1F): *Head:* frons with a tuft of dark brown hair; eyes blackish-brown, smooth; labial palpi covered with blackish-brown hair; antennae dorsally chestnut, ventrally rufous, with white scales at the base of each segment, club dorsally slightly darker than shaft. *Thorax:* dorsal and ventral surface dark brown; legs paler yellowish-brown. *Abdomen:* dorsal and ventral surface dark brown. *Wings:* forewing (length: 17.5-20.5 mm; mean: 19 mm; n=12) distal margin convex, apex rounded to subacute; hindwing rounded with weakly pronounced notch at tornus. DFW medium brown. DHW medium brown, slightly darker towards base, with pale postdiscal band from apex to tornus indistinctly showing from ventral surface. VFW ground colour medium brown, becoming slightly paler from base to apex; very faint, thin, straight, darker brown postdiscal line, parallel to distal margin, in cells Cu2-Cu1 to M1-R5; a row of faint, pale postdiscal spots in center of cells Cu2-Cu1 to M2-M1 gently curved basally, in some individuals outer spots indistinct; thin, faint, uneven (but not zigzag), darker brown submarginal line from apex to tornus. VHW medium brown, slightly paler towards distal margin; straight, cream-colored postdiscal band from costa to tornus through base of cell Cu1-M3; thin, faint, slightly uneven (but not zigzag), darker brown submarginal line from apex to tornus. *Male genitalia* (Fig. 10D): uncus smoothly arching, subunci relatively long, valvae short and squat with numerous 'teeth' at distal tip, some extending towards base, and

dense cluster of 'teeth' at dorsal edge of valva near base; aedeagus shallowly curving dorsally, with several short, posteriorly directed spines laterally near middle.

FEMALE (Fig. 1G): Similar to male except slightly larger (forewing length 21 mm) and lighter coloured on both wing surfaces.

Types: Holotype male: ECUADOR: Cotopaxi, Pilaló, 2750-3000 m, VII.1996, I. Aldas *leg.*, MZUJ; **Allotype female:** same data as the holotype except 1997, TWP; **Paratypes (76 males and 6 females):** ECUADOR: 3 **males:** Pichincha, San Juan-La Victoria road, 3200 m, 30.I.2002, T. Pyrcz *leg.*, TWP (2), MUSM (1); 1 **male:** same locality, 2900-2950 m, 01.II.2002, T. Pyrcz *leg.*, TWP; 2 **males:** same locality, 3350 m, II.2002, I. Aldas *leg.*, TWP; 2 **males:** Pichincha, Aloag-Tandapi road, km 13, 3000-3050 m, II.2002, I. Aldas *leg.*, TWP; 2 **males:** Pichincha, Aloag-Tandapi road, Sector Los Alpes, 2700-2750 m, 26.I.2004, T. Pyrcz & R. Garlacz *leg.*, TWP; 1 **male:** Pichincha, Volcán Pasochoa 2600-2750, 22.VIII.2003, T. Pyrcz *leg.*, TWP; 2 **males:** Cotopaxi, Pilaló, 2750-3000 m, VII.1996, I. Aldas *leg.*, TWP (1), MECN (1); 1 **male:** Pichincha, old Quito - Sto. Domingo rd. 2700m, 12.VIII.1993, J. Hall *leg.*, KWJH; 1 **male:** Pichincha, Yanacocha, Volcán Pichincha, 3500 m, 18.IX.1997, K. Willmott *leg.*, KWJH; 4 **males:** Tungurahua, Triunfo - Patate, El Tablón, 3000 m, 21.XI.1998, P. Boyer *leg.*, TWP (1), PB (3); 2 **males:** Tungurahua, Triunfo - Patate, El Tablón, 3000 m, I.1999, I. Aldas *leg.*, TWP; 3 **males:** Tungurahua, Baños, Runtún, 3000 m, III.1999, I. Aldas *leg.*, TWP; 2 **males:** Tungurahua, Baños, Pondoá, 3365 m, 19.I.2002, J. Wojtusik & R. Garlacz *leg.*, TWP; 32 **males:** Tungurahua, Baños, El Tablón, 3000 m, III.1999, I. Aldas *leg.*, MBLI; 5 **males:** Tungurahua, Baños, 3000 m, III.1999, I. Aldas *leg.*, MBLI; 1 **male:** Morona-Santiago, Gualaceo-Limón road, 3100 m, 09.II.2002, T. Pyrcz *leg.*, TWP; 1 **male:** same locality, 3100 m, 09.III.1998, P. Boyer *leg.*, TWP; 1 **male:** Carchi, Tulcán-Maldonado, Volcán Chiles, 3000-3050 m, 27.VIII.2004, T. Pyrcz *leg.*, TWP; 1 **male:** Carchi, near Huaca, 2900-3200 m, III.1999, I. Aldas *leg.*, MBLI; 1 **female:** Pichincha, San Juan-La Victoria, 3300-3400 m, 30.I.2002, T. Pyrcz *leg.*, TWP; 1 **female:** Tungurahua, Triunfo-Patate, El Tablón, 3000 m, 21.IX.1998, P. Boyer *leg.*, TWP; 1 **female:** Tungurahua, Baños, Runtún, 3000m, VIII.1998, I. Aldas *leg.*, TWP; 1 **female:** Tungurahua, Runtún, 2900-2950 m, 21.I.2002, J. Wojtusik, *leg.*, TWP; 1 **female:** Tungurahua, Baños, El Tablón, 3000m, III.1999, I. Aldas *leg.*, MBLI; COLOMBIA: 5 **males:** Cauca, Volcán Puracé, Termales de San Juan, 3150-3200 m, 28-30.III.1996, T. Pyrcz *leg.*, TWP; 1 **male:** Caldas, Páramo de Letras, 23.VII.1993, J-F. Le Crom *leg.*, TWP; 2 **males:** Antioquia, El Retiro, 2300-2800 m, 26-30.VIII.2003, G. Rodríguez *leg.*, TWP; 1 **male:** Antioquia, El Retiro, Reserva San Sebastián, 2500-2800 m, 12.IX.2003, T. Pyrcz *leg.*, TWP; 1 **female:** Antioquia, El Retiro, 2300-2800 m, 18-25.VII.2003, G. Rodríguez *leg.*, TWP.

Etymology: This species is named after the Ecuadorian entomologist, Germania Estévez, formerly of the Museo Ecuatoriano de Ciencias Naturales in Quito, in recognition of her help during our research in Ecuador.

Comments: *Manerebia germaniae* occurs at high elevations, near or at the tree-line, and has been recorded in Ecuador from 2700-3500 m. The nominate subspecies is widespread along the central Andean ridge from Colombia (Antioquia) to south-central Ecuador, where it occurs on both Andean slopes (Fig. 15). It is associated with intact cloud forest and remnant scrub. In western Ecuador (Pichincha, Cotopaxi) it generally replaces the local subspecies of *M. inderena* at higher elevations, but there is a narrow elevational band where the two occur in sympatry, generally between 2800-3100 m.

Manerebia germaniae vitalei Pyrcz & Willmott, n. ssp.

Figs. 1H, 10E, 15

Manerebia n. sp., n. ssp. (Pyrcz, Willmott & Hall); Lamas & Viloria (2004: 216, n. I123b).

Diagnosis: In this taxon the VHW yellow postdiscal band is

approximately 1.5 times the width of that of the nominate subspecies.

Description: MALE (Fig. 1H): **Head, thorax and abdomen:** as in the nominate subspecies. **Wings:** Forewing (length: 19.5 mm; mean: 19.5 mm; n=2) distal margin very slightly convex, apex subacute; hindwing rounded with weakly pronounced notch at tornus. DFW surface medium brown. DHW medium brown; pale postdiscal band from apex to tornus indistinctly showing from ventral surface. VFW ground colour medium brown, slightly lighter in submarginal area; very faint, thin, darker brown postdiscal line, straight and parallel to outer margin from vein R5 to Cu2, then curving towards tornus; a row of faint, barely visible pale yellow postdiscal spots in center of cells Cu2-Cu1 to M2-M1; thin, faint, uneven (but not zigzag), darker brown submarginal line from apex to tornus. VHW medium brown, slightly paler towards distal margin; straight, approximately 2mm wide, cream-colored (with an orange shade towards anal margin) postdiscal band from costa to tornus through base of cell Cu1-M3; occasional 3 to 4 minute pale yellow postdiscal spots; faint, slightly uneven (but not zigzag), darker brown submarginal line from apex to tornus. **Male genitalia** (Fig. 10E): similar to that of the nominate subspecies.

FEMALE: Unknown.

Types: Holotype male: ECUADOR: Loja, OSId road Loja - Zamora, 2500 m, XI-XII.1999, I. Aldas *leg.*, ex MBLI, MZUJ. **Paratype male:** same data as the holotype, MBLI.

Etymology: This subspecies is dedicated to the Italian lepidopterist Fabio Vitale, from Lecce, who specializes in the Ithomiinae.

Comments: This subspecies consistently differs from the nominate throughout its range in the width of the VHW postdiscal band. It is the southernmost representative of *M. germaniae*, and is known to date only from the eastern slopes of the Ecuadorian Andes in the province of Zamora-Chinchipec (Fig. 15), though it may also extend into extreme northern Peru.

Manerebia pluviosa Pyrcz & Viloria, n. sp.

Figs. 2A, 10F, 15

Manerebia n. sp. (Pyrcz & Viloria); Lamas & Viloria (2004: 216, n. I120).

Diagnosis: This species is easily distinguished from any congener by the wide yellow postdiscal band on both fore- and hindwing dorsal and ventral surface.

Description: MALE (Fig. 2A): **Head:** frons with a tuft of dark brown hair; labial palpi covered with short dark brown hair; eyes dark brown, smooth; antennae dark brown dorsally, chocolate brown ventrally with white scales at base of each segment, club twice as wide as shaft, of same colour. **Thorax:** dorsally dark brown, hairy, ventrally pale brown; legs paler yellowish-brown. **Abdomen:** dorsally dark brown, laterally and ventrally pale brown. **Wings:** Forewing (length: 19 mm, n=2) triangular; tornus slightly obtuse. Hindwing rounded, anal margin slightly excavated near tornus. Dorsal ground colour uniform chocolate brown, except for entire postdiscal yellow band on both wings, more distinct on hindwing; basal half and anal region of hindwing with long thin brown hairs. VFW colour pattern similar to dorsal surface but in general more intense; postdiscal band more distinct and wider, reaching tornus; submarginal and marginal regions lighter brown. VHW similar to dorsal surface but more intense in colour; postdiscal band slightly broadened towards central portion; series of four submarginal white dots in cells M2-M3 to Cu2-1A, respectively, the first one half diameter of others, which are ca. 0.8 mm. **Male genitalia** (Fig. 10F): uncus arched, valva with spiny dorsal process near base, aedeagus short.

FEMALE: Unknown.

Types: Holotype male: VENEZUELA: Táchira, Parque Nacional El Tamá, entre Betánia y La Banderola, 2810 m, 23.VIII.1996, A. Viloria *leg.*, MALUZ. **Paratype male:** VENEZUELA: Táchira, Parque Nacional El Tamá, Fundo Piedra Blanca, San Vicente de la Revancha, 2400 m, 9-12.XII.1997, F. Rey *leg.*, TWP.

Etymology: The name is the feminine form of the Latin adjective "pluviosus", meaning rainy. The male holotype was collected while flying very weakly during heavy rain in the upper cloud forest of the Sierra de El Tamá.

Comments: The male genitalia of this species are most similar to those of *M. leaena* and *M. germaniae*, with an arched uncus and spiny process at the dorsal base of the valva. In *M. pluviosa* the narrow dark VHW submarginal line is smoothly curving, not dentate like *M. leaena*, and in this respect resembles that of *M. germaniae*, which may prove to be its sister species. *Manerebia pluviosa* occurs in the Sierra de El Tamá in habitats similar to those of *M. germaniae*, close to the tree-line, and possibly replaces *M. leaena gonzalezi* at higher elevations. The paratype was collected in disturbed habitat in San Vicente de la Revancha at an elevation that is probably beneath that at which the species usually occurs. *Manerebia pluviosa* is extremely similar (though about half the size) to the microsympatric pronophiline *Pedaliodes* sp. Pyrcz & Vilorio (in press), though it is not clear whether this similarity results from mimicry, and if so, what the basis for this mimicry might be. Some 30 years ago *M. pluviosa* was also captured by J. Bechyné, at 3100 m in the páramo of a remote mountain range in the north Colombian department of Norte de Santander (Cerro Oroque), where no other butterflies have since been collected. That specimen shows some distinctive characters and might represent a separate subspecies, so it is therefore excluded from the type series. This species seems to be a rare insect and has only been recorded during the wet season.

Manerebia apiculata (C. & R. Felder, 1867)

Figs. 2B,C, 11A, 15

Pronophila apiculata C. & R. Felder (1867: 474). **TL:** Colombia, Cundinamarca, Bogotá. **ST male:** "apicu-lata Feld/Felder Colln./Rothschild Bequest B.M. 1939-1/4/Bogota Lindig type/Type". BMNH(R) [examined].

= *Lymanopoda apiculata* form *curvilinea* Weymer (1912: 248). **TL:** Colombia, East Cordillera, Cundinamarca, Boquerón de C(h)ipaque. **ST male(s):** ZMHU? [not located].

Lymanopoda apiculata (C. & R. Felder); Weymer (1911: pl. 53, row a (*apiculata* [sic])); 1912: 248).

Penrosada apiculata (C. & R. Felder); Brown (1944: 257, pl. 1, fig. 1622) (male genitalia); Pyrcz (1999: 367).

Manerebia apiculata (C. & R. Felder); Lamas & Vilorio (2004: 215).

Diagnosis: The male genitalia (Fig. 11A) of this species are similar to those of *M. leaena*. The species is easily distinguished externally from all other sympatric *Manerebia* in the Colombian Cordillera Oriental by the acute forewing apex. The expression of the VHW band is variable, exhibiting a similar polymorphism to the Ecuadorian *M. interrupta* (Fig. 6E,F,G) and *M. ignilineata* (Fig. 7D,E,F). The syntype specimen in the BMNH lacks any VHW post-discal band, while the form in which the band is fully developed flies with typical specimens (Adams, 1986) and was named form *curvilinea* by Weymer (1912) (Lamas & Vilorio, 2004). Although we have not located any types of *curvilinea*, the description clearly applies to this form of *M. apiculata*, which cannot be confused with any other *Manerebia* species from the region of the type locality.

Comments: This species inhabits the forest/páramo ecotone on both slopes of the central Cordillera Oriental in Colombia (Cundinamarca: Sibate, Fusagasugá, Facativá), from 3150-3300 m, where it occurs with *M. levana* (Adams, 1986).

Manerebia franciscae (Adams & Bernard, 1981)

This species is most closely related to *M. mam-muthus* n. sp., *M. satura* and *M. navarrae*, and all four species are allopatric. The males of all of these species

are unique among north Andean *Manerebia* in having a distinct dark brown patch of androconial scales on the DFW in the posterior third of the discal cell and basal part of cells 1A-Cu2 to M2-M1 (Figs. 2, 3). The male genitalia are also similar, with an arched uncus, relatively long subunci and valva with a spiny dorsal process near the base, similar to *M. leaena* and related species (Figs. 10, 11; see Discussion under that species). *Manerebia franciscae* differs from the two neighbouring species *M. navarrae* and *M. mam-muthus* in having an almost smooth aedeagus, with only a few spines on the left side. Other differences are discussed under those two species. It differs from *M. satura* in the narrower, distal process of the valva being relatively longer, with the mid-ventral edge of the valva more indented.

There is geographic variation in the presence or absence of the pale VHW postdiscal band, as in *M. satura*, and two subspecies are recognised.

Manerebia franciscae franciscae (Adams & Bernard, 1981)

Figs. 2D, E, 11B, 16

Penrosada franciscae Adams & Bernard (1981: 365, figs 11, 25, 26). **TL:** Venezuela, Mérida, above La Montaña, S. of Mérida. **HT male:** BMNH(A&B) [examined].

Manerebia franciscae (Adams & Bernard); Lamas & Vilorio (2004: 215).

Diagnosis: This subspecies is superficially most similar to *M. inderena inderena*, with which it occurs, but the large tornal and apical ocelli on the VHW, with those in the middle of the wing reduced, are diagnostic.

Comments: Contrary to the statement of Adams & Bernard (1981), this taxon is not restricted to the Venezuelan Cordillera de Mérida, but also occurs in the Sierra de El Tamá and on the western slopes of the Cordillera Oriental in Colombia (Pacho, TWP, SMTD) (Fig. 16). Adams & Bernard (1981) report that *M. f. franciscae* flies with a skipping action, usually more than 2 m above the ground, and rests on foliage. Eggs are laid on the brownish petioles of young leaflets, near the nodes of *Chusquea* bamboo canes, from 1-4 m above the ground. The species was seasonally common at the type locality, and Adams & Bernard (1981) collected it from 2300-2600 m. We have also found the species to be seasonal, only observing and collecting it in the Cordillera de Mérida in the rainy season from June to September (Pyrcz, pers. obs.).

Manerebia franciscae rodriguezi Pyrcz & Willmott, n. ssp.

Figs. 2F,G, 11C, 16

Diagnosis: This taxon differs from nominate *M. franciscae* primarily by the absence of VHW yellow postdiscal band. The apical ocelli on the VHW are also reduced, the yellowish rings surrounding the VHW ocelli are indistinct, and the dark, thin submarginal lines on the VFW and VHW are slightly reddish.

Description: MALE (Fig. 2F): **Head, thorax** and **abdomen** same as in the nominate subspecies. **Wings:** Forewing (length: 21.5-22 mm; mean: 21.7; n=3) distal margin straight to slightly convex, apex rounded; hindwing rounded with almost no notch at tornus. DFW chocolate brown; darker brown androconial scales occupying posterior one-third of discal cell, basal half of cells 1A-Cu2, basal third of cell Cu1-M3, and basal quarter of cells M3-M2 and M2-M1.

DHW uniform chocolate brown; occasionally one small black submarginal white oval dot ringed with black in Cu1-Cu2 and two, even smaller, in 1A-Cu2. VFW ground colour medium brown becoming paler and lighter towards distal half; thin, irregular reddish brown submarginal line, parallel to distal margin and very thin, reddish brown marginal line parallel to outer margin, from apex to tornus. VHW uniform medium brown; very faint, darker brown, straight postdiscal line from apex to anal margin near tornus; uneven, faint submarginal reddish brown line and reddish brown marginal line; small, white, oval submarginal dots in cell Cu2-Cu1, and two in cell 1A-Cu2, ringed with black. **Male genitalia** (Fig. 11C): uncus long and arched; subunci long and thin; numerous small spines on distal tip of valva extending anteriorly along dorsal edge, dorsal base of valva with a projection with two 'teeth'; aedeagus length of valva, slightly curved.

FEMALE (Fig. 2G): Slightly larger than male (forewing length 23 mm), with more prominent white dots on ventral surface occasionally taking shape of fully developed ocelli, particularly in cell Cu1-M3 on VFW, showing through on dorsal surface, and additionally with minute submarginal white dots present in most cells of fore and hindwing.

Types: *Holotype male*: COLOMBIA: Antioquia, Guarné, 2600-2650 m, 14.III.1997, G. Rodríguez leg., MZUJ; *Allotype female*: Antioquia, El Retiro, 1800 m, 19.VIII.2002, G. Rodríguez leg., TWP; *Paratypes* (4 males and 2 females): COLOMBIA: 1 male: Antioquia, no data, G. Rodríguez leg., GR; 1 male: Antioquia, El Retiro, Río Agudelo, 2400 m, VII.1999, G. Rodríguez leg., GR; 1 male: Antioquia, El Retiro, 2800 m, 24.VI.2001, G. Rodríguez leg., GR; 1 male: Antioquia, El Retiro, 2200-2600 m, 20.VIII.2003, G. Rodríguez leg., MZUJ; 1 female: Antioquia, Envigado, 2600 m, 29.XI.2002, G. Rodríguez leg., GR; Antioquia, Santa Elena, Represa de Piedras Blancas, 2600m, 15.IX.2003, Rodríguez leg., GR.

Etymology: This subspecies is named after its first collector, Gabriel Rodríguez from Medellín.

Comments: This taxon is associated with *M. franciscae* based on similar male genitalia and VHW pattern, with characteristic submarginal white dots in cells Cu2-Cu1 and 1A-Cu2. *Manerebia franciscae rodriguezi* is apparently endemic to the northern Cordillera Central in Colombia, where it occurs in mid-elevation cloud forest, similar to the nominate subspecies.

Manerebia mammuthus Pyrcz & Willmott, n. sp.

Figs. 2H, 11D, 16

Manerebia n. sp. (Pyrcz, Willmott & Hall); Lamas & Viloria (2004: 216, n. 1127).

Diagnosis: This species is distinguished from its closest relatives, *M. franciscae* and *M. satura* (see Discussion under *M. franciscae*), by its large size, the virtual absence of any ventral submarginal ocelli and characters of the male genitalia. The aedeagus has a large patch of dense, tiny spines on both sides, while *M. franciscae* and *M. satura* have at most a single lateral line of spines on each side or are smooth. The narrower distal portion of the valva is relatively shorter than in *M. franciscae*, and the mid-ventral edge of the valva is indented, like *M. franciscae* but not *M. satura*, in which it is flatter.

Description: **MALE** (Fig. 2H): **Head:** frons with a tuft of dark brown hair; eyes blackish-brown, smooth; labial palpi covered with blackish-brown hair; antennae dorsally chestnut, ventrally rufous, with white scales at the base of each segment, club dorsally slightly darker than shaft. **Thorax:** dorsal and ventral surface dark brown; legs paler yellowish-brown. **Abdomen:** dorsal and ventral surface dark brown. **Wings:** forewing (length: 22.5-24 mm, mean: 23.3 mm, n=2) distal margin convex, apex rounded; hindwing rounded with almost no notch at tornus. DFW medium brown; darker brown androconial scales occupying posterior half of discal cell, basal half of cells 1A-Cu1, basal third of cell Cu1-M3, and basal quarter of cell M3-M2. DHW medium brown, slightly darker towards base, with pale postdiscal band from apex to tornus indistinctly show-

ing from ventral surface. VFW ground colour medium brown, becoming slightly paler from base to apex; very faint, thin, straight, darker brown postdiscal line, parallel to distal margin, in cells 1A-R5; three whitish postdiscal dots in centers of cells Cu1-M1; thin, faint, uneven, darker reddish brown submarginal line from apex to tornus; margin thinly lined with darker brown. VHW medium brown; thin, straight, yellowish cream-colored postdiscal band from costa to tornus through base of cell Cu1-M3; thin, faint, zigzag, darker reddish brown submarginal line from apex to tornus; tiny white submarginal dots in centers of cells 1A-M2. **Male genitalia** (Fig. 11D): uncus long and smoothly arching; subunci relatively long; valvae thinning gradually at middle towards posterior tip, dorsally grooved, with 4-6 'teeth' at distal tip and several additional 'teeth' extending basally along inner edge; thin, pointed projection at dorsal edge of valva near base, with numerous tiny spines; aedeagus curving dorsally, with patches of numerous short, posteriorly directed spines laterally near middle, on both sides.

FEMALE: Unknown.

Types: *Holotype male*: ECUADOR: Sucumbíos, km 9 La Bonita-Tulcán rd., El Higuerón, 2200 m, 10.XI.1997, K. Willmott leg., to be deposited in AME; *Paratypes* (3 males): ECUADOR: 1 male: same data as the holotype, KWJH; COLOMBIA: 1 male: same locality as the holotype, 2000-2400 m, X.2001, I. Aldas leg., ex MBLI, TWP; 1 male: same data as preceding, MBLI.

Etymology: The specific name is a noun in apposition derived from the elephant genus *Mammuthus*, with reference to this species' large size, almost uniform brown coloration and elongate uncus and subunci, resembling the trunk and tusks of these extinct creatures.

Comments: We deliberated as to whether to treat this taxon as a subspecies of either *M. satura* or *M. franciscae*. However, the number of consistent wing pattern and genitalic differences between these three species suggest they should be maintained. In addition, it appears to occur at higher elevations than *M. satura*. This species is known from only four specimens, all collected in far northeastern Ecuador along the valley of the Río Chingual along a trail through secondary growth, with large tracts of undisturbed forest within 50 m distance, from 2000-2400 m. The two males collected by KW were encountered on the same day puddling on wet sand and feeding on horse dung. Despite a number of other visits to the same locality the species has only been seen on two occasions.

Manerebia satura (Weymer, 1911)

Figs. 3A, 11G

Lymanopoda leaenavar. satura Weymer (1911: pl. 52, row f; 1912: 249). **TL:** Peru, Cuzco; Colombia, Tolima, Quindiu Pass. **ST male(s):** ZMHU? [not examined].

Penrosada satura (Weymer); Brown (1944: 258) (status uncertain).

Manerebia satura (Weymer); Lamas & Viloria (2004: 216).

This is a large species, closely related to the allopatric *M. franciscae*, *M. mammuthus* and *M. navarrae*, as discussed under *M. franciscae*. The male genitalia are distinctive, with the distal, narrower portion of the valva being relatively short, and often only bearing a few large spines, rather than numerous smaller spines. Unlike *M. mammuthus*, the aedeagus is smooth or has only a single lateral line of spines. It is the most widespread member of the genus and it is fairly polytypic, occurring along the eastern slopes of the Andes from Bolivia to Ecuador in lower to mid-elevation cloud forests.

Manerebia satura was described based on specimens

from two localities, Cuzco (Peru) and Quindiu Pass (Colombia), representing two distinct species. The specimen figured in the original description represents the species as treated here, while those from Colombia are actually *M. inderena* Adams (see Adams, 1986), which also has a white VHW band but is smaller, with smaller VHW ocelli, and is not closely related to *M. satura*. The syntype specimen(s) should be in the ZMHU (G. Lamas, pers. comm.), but despite some searching we have been unable to locate any. For the present we do not designate either a lectotype or neotype, since the type specimens may yet be found, but our usage of the name preserves nomenclatural stability, as should any future type designation. The nominate subspecies, distinguished by the wide white VHW postdiscal band and large tornal and apical ocelli, particularly in cell Cu2-Cu1 (Fig. 3A), occurs in southern Peru only (Cuzco, Puno, perhaps to northern Bolivia). An undescribed subspecies of *M. satura*, characterised by a yellow VHW band, occurs from central Peru (Junín, Pasco) to northern Peru (San Martín, Amazonas) (Pyrz, in prep.). In extreme northeastern Peru in the Cordillera del Cóndor, and in eastern Ecuador, occur two distinct subspecies, described below.

***Manerebia satura lamasi* Pyrcz & Willmott, n. ssp.**

Figs. 3B, 11F, 16

Diagnosis: This subspecies is larger than the similar and neighbouring *M. s. pauperata* (described below), darker brown on both wing surfaces, with smaller ocelli on the VHW and a small ocellus in cell M1-M2 on the VFW. There is no slightly paler brown postdiscal line and the narrow, dark submarginal lines are less marked.

Description: MALE (Fig. 3B): *Head*, *thorax* and *abdomen* as in *M. satura pauperata*. *Wings:* forewing (length: 22.5-23.5 mm; mean: 23 mm; n=3) distal margin straight, apex rounded; hindwing rounded with very weakly pronounced notch at tornus. DFW dark brown; androconial scales occupying posterior half of discal cell, basal half of cells 1A-Cu1, basal third of cell Cu1-M3, and basal quarter of cell M3-M2. DHW uniform dark brown, with two small submarginal black ocelli thinly ringed with yellow in cells 1A-Cu2 and Cu2-Cu1; a barely visible submarginal blackish line. VFW ground colour dark brown, slightly lighter along outer margins; tiny black submarginal ocelli with white pupils in cells M2-M1, Cu2-Cu1 (and in M1-R5 in one individual); faint, black submarginal line from tornus to apex; two thin, straight, dark brown marginal lines. VHW uniform dark brown; barely visible straight, thin, blackish postdiscal line from tornus to apex, joining with a better marked, blackish submarginal line that is smoothly curving and parallel to distal margin; black submarginal ocelli, ringed with dark yellow, with white pupils, as follows: two small in cell 1A-Cu2, one larger in cell Cu2-Cu1 (half width of cell), one in cell M2-M1, one small in cell M1-Rs, and tiny white dots in cells Cu2-M3; thin, blackish marginal line close to and parallel with distal margin. *Male genitalia* (Fig. 11F): uncus long and arched; subunci relatively long; valva thinning gradually throughout from base to posterior tip, dorsally grooved, with 6 'teeth' at distal tip; wide, toothed projection at dorsal edge of valva near base; saccus shallow; aedeagus short, slightly curved dorsally and smooth.

FEMALE: Unknown.

Types: *Holotype male:* PERU: Amazonas, Cordillera del Cóndor,

2-3 km N PV3 (Alfonso Ugarte), 0345/7826, 1600-1750 m, 22.VII.1994, G. Lamas *leg.*, MUSM; *Paratypes:* 2 males: same data as the holotype, MUSM.

Etymology: This subspecies is named for Gerardo Lamas, the collector of the type series, in gratitude for all his help and correspondence over many years.

Comments: *Manerebia satura lamasi* appears to be endemic to the Cordillera del Cóndor. Other pronophilines that are also apparently endemic to this mountain range include *Manerebia magnifica* n. sp. (described below), which occurs in the same area but at lower elevations, and an undescribed species of *Panyapedaliodes* Forster, 1964 (Viloria & Lamas, in prep.).

***Manerebia satura pauperata* Pyrcz & Willmott, n. ssp.**

Figs. 3C,D, 11E, 16

Euptychia jovita (C. & R. Felder); D'Abrera (1988: 778) (misidentification).

Penrosada sp.; D'Abrera (1988: 824) (misidentification).

Manerebia satura n. ssp. (Pyrz, Willmott & Hall); Lamas & Viloria (2004: 216).

Diagnosis: Males of this subspecies are distinguished from all other *M. satura* subspecies, except *M. s. lamasi*, by the absence of the pale VHW postdiscal band. In females the band is well-developed and chalky white, but specimens may easily be identified by the large ocellus in cell Cu2-Cu1 that is visible on the dorsal surface of both wings. The characters that distinguish this subspecies from *M. s. lamasi* are discussed under that taxon.

Description: MALE (Fig. 3C): *Head:* frons with a tuft of dark brown hair; eyes blackish-brown, smooth; labial palpi covered with blackish-brown hair; antennae dorsally chestnut, ventrally rufous, with white scales at the base of each segment, club dorsally slightly darker than shaft. *Thorax:* dorsal and ventral surface dark brown; legs paler yellowish-brown. *Abdomen:* dorsal and ventral surface dark brown. *Wings:* forewing (length: 19.5-22 mm; mean: 20.7 mm, n=10) distal margin straight, apex rounded; hindwing rounded with very weakly pronounced notch at tornus. DFW medium brown; darker brown androconial scales occupying posterior half of discal cell, basal half of cells 1A-Cu1, basal third of cell Cu1-M3, and basal quarter of cell M3-M2. DHW medium brown, slightly darker towards base, with two submarginal black ocelli ringed with yellow in cells 1A-Cu2 and Cu2-Cu1. VFW ground colour medium brown, becoming slightly paler from base to distal margin; thin, straight, darker brown postdiscal line, parallel to distal margin, in cells 1A-R5; a tiny black submarginal spot ringed with yellow in cell Cu2-Cu1; distinct, uneven, darker brown submarginal line from tornus to apex, becoming more undulate towards apex; two thin, straight, dark brown marginal lines. VHW medium brown, darker in basal half; distinct, thin, darker brown postdiscal line from tornus to apex, joining with a distinct, darker brown submarginal line that is smoothly curving and parallel to distal margin; black submarginal ocelli, ringed with dark yellow, with white pupils, as follows: two small in cell 1A-Cu2, one large in cell Cu2-Cu1 (almost width of cell), one medium in cell M2-M1, one small in cell M1-Rs, and tiny white dots in cells Cu2-M3; thin, dark brown marginal line close to and parallel with distal margin. *Male genitalia* (Fig. 11E): uncus long and smoothly arching; subunci relatively long; valvae thinning gradually throughout from base to posterior tip, dorsally grooved, with 4-6 'teeth' at distal tip; thin, rounded projection at dorsal edge of valva near base; aedeagus curving dorsally, with a row of several short, posteriorly directed spines laterally near middle, on each side.

FEMALE (Fig. 3D): Differs from male as follows: larger (slightly length: 22-23 mm; mean: 22.5 mm, n=2) paler brown throughout. DFW lacking androconial scales, with large submarginal black, yellow-ringed ocellus with white pupil in cell Cu2-Cu1. DHW with ventral ocelli visible in cells 1A-Cu2, Cu2-Cu1, Cu1-M3, and M2-M1. VFW with similar large ocellus in cell Cu2-Cu1, with yellow

ring extending into cells anterior and posterior, and tiny white submarginal dots in cells Cu1-M1. VHW with broad, chalky white postdiscal band posterior to dark brown postdiscal line, broadest in cells 1A-Cu2 and Cu2-Cu1, ocellus in cell M1-Rs larger.

Types: *Holotype male*: ECUADOR: Zamora-Chinchipe, Loja - Zamora km 40, 1500 m, 31.VIII.1990, P. Gros & S. Attal, MZUJ; *Allotype female*: same data as the holotype, MZUJ; *Paratypes (10 males and 2 females)*: ECUADOR: **1 male and 1 female**: Zamora-Chinchipe, Loja-Zamora rd., nr. Sabanillas, Quebrada San Ramón, 1700 m, 27-29.X.1997, K. Willmott *leg.*, KWJH; **2 males**: Zamora-Chinchipe, Zamora-Loja rd., 1800 m, 9.XI.1996, K. Willmott *leg.*, KWJH (1), MECN (1); **1 female**: Zamora-Chinchipe, Loja - Zamora km 40, 1500 m, 01.IX.1990, P. Gros & S. Attal, TWP; **3 males**: same data as the holotype, TWP; **1 male**: same data but 03.IX.1990, TWP; **1 male**: same data but 08.XI.1996, TWP; **1 male**, Zamora-Chinchipe, West of Valladolid, 1800 m, 22.IV.1997, A. Jasiński *leg.*, TWP; **1 male**: Zamora-Chinchipe, Valladolid, 25.VII.1992, G. Estévez, MECN; **1 male**: Tungurahua, Machay, 17.X.1994, I. Aldas *leg.*, TWP.

Etimology: The name is the feminine form of the Latin adjective "pauperatus", meaning impoverished, with reference to the absence of the pale ventral hindwing postdiscal band in males, in comparison with the nominate subspecies.

Comments: This taxon was illustrated twice by D'Abrera (1988) as *Penosada* sp. (p. 824) and as *Euptychia jovita* (p. 778). It apparently occurs from northeastern (Napo - one male in coll. TWP from Cordillera de Huacamayos, no date, A. Jasiński *leg.*, Tungurahua) to southeastern (Zamora-Chinchipe) Ecuador (Fig. 16), although it is more common in the south, and has been collected in cloud forest habitats in a narrow elevational band from 1500-1800 m. The specimen from Cordillera de los Huacamayos is excluded from the type series since it shows slight differences to southern specimens. We have found males puddling along forested streams, and a single female flying low to the ground in a small field at the forest edge.

Manerebia navarrae (Adams & Bernard, 1979)

Figs. 3E, 11H, 16

Penosada navarrae Adams & Bernard (1979: 114, figs 11, 32). **TL:** Colombia, César, Serranía de Valledupar, 2300 m. **HT male:** BMNH(A&B) [examined].

Manerebia navarrae (Adams & Bernard); Lamas & Viloria (2004: 215).

Diagnosis: This species superficially resembles several other *Manerebia* that lack the pale VHW postdiscal band, but may be distinguished by the orange wedge extending basally from the VHW postdiscal line at the tornus, and by the ocellus in cell Cu2-Cu1, which is absent in the superficially similar *M. quinterae*. The male genitalia (Fig. 11H) are distinctive in the dorsal process at the base of the valva being more elongate than in other species, while the thickened, strongly curved aedeagus with a dense patch of spines on the right side only is unique.

Comments: This species appears to be most closely related to *M. satura*, *M. mammuthus* and *M. franciscae*, as discussed under the last of these species. It is known only from the type locality in the Serranía de Valledupar in the Sierra de Perijá range on the Colombia/Venezuela border, at 2300 m. Adams & Bernard (1979) state that the entire type series was caught before 10:00 hrs, flying around a single patch of bamboo.

Manerebia quinterae (Adams & Bernard, 1979)

Figs. 3F, 11I, 16

Penosada quinterae Adams & Bernard (1979: 115, figs 12, 33, 34). **TL:** Venezuela, Zulia, Serranía de Valledupar, 3050 m. **HT male:** BMNH(A&B) [examined].

Manerebia quinterae (Adams & Bernard); Lamas & Viloria (2004: 215).

Diagnosis: The ventral surface of *M. quinterae* (Fig. 3F) somewhat resembles that of *M. navarrae*, but *M. quinterae* may be easily distinguished by the irregular dark postdiscal line, lack of any well developed submarginal ocelli, and instead a submarginal line of whitish spots in cells Cu2-M1. The male genitalia (Fig. 11I) are distinctive in lacking a spiny dorsal process at the base of the valva, unlike all preceding species, but notably have an arched uncus, like many of the preceding species. The affinities of this species are therefore unclear. The small, lateral patches of spines on both sides of the aedeagus near its posterior tip are distinctive.

Comments: Adams & Bernard (1979) reported that this species occurred from 2750-3050 m in the Serranía de Valledupar, where it could be locally and seasonally common. It is known to date only from the type locality.

Manerebia inderena (Adams, 1986)

The male genitalia of this species do not differ from those of *M. golondrina* n. sp., which can be immediately recognised by the lack of a VHW postdiscal yellow or white band, and are also similar to *M. prattorum* n. sp. These three species can be distinguished from other species by the simple valva (lacking a prominent spiny process at the dorsal edge near the base), the uncus which is strongly "bent" near the base (almost straight in *M. undulata* n. sp., *M. trimaculata* and *M. interrupta*), then approximately straight (smoothly curving in *M. rufanalis*), and in usually having several tiny 'teeth' on the left hand side of the aedeagus. The VHW narrow dark submarginal line is irregularly zigzag, but never as undulate as in *M. undulata* or parallel to the distal margin as in *M. germaniae*.

This is a widespread and polytypic species. The various taxa are grouped together on the basis of similar genitalia, habitat and elevation, and close range allopatry. Reasons for considering *M. golondrina* a distinct species are discussed under that species.

Manerebia inderena inderena (Adams, 1986)

Figs. 3G,H, 12A, 17

Penosada inderena Adams (1986: 305). **TL:** Colombia, Tolima, south above Cajamarca. **HT male:** BMNH(A&B) [examined].

Manerebia inderena (Adams); Lamas & Viloria (2004: 215).

Diagnosis: The nominate subspecies (Fig. 3G,H) is characterized by medium wide, whitish VHW postdiscal band, that is yellow and usually thinner in *M. i. antioquiensis*, white and much thinner in *M. i. fina*, whitish and wider in *M. i. clara*, wider and yellow in *M. i. mirena*, *M. i. leaeniva* and *M. i. similis*. The nominate subspecies and *M. i. antioquiensis* may also be distinguished from other similar species (*M. germaniae*, *M. leaena*, *M. franciscae*) by the three marked submarginal ocelli in cells 1A-Cu2 and Cu2-Cu1 only. Male genitalia as illustrated (Fig. 12A).

Comments: Adams (1986) stated that this taxon could be found skipping around clumps of bamboo, resting on the foliage, and occasionally descending to feed on excrement on the ground. In Colombia it has been found in the Cordillera Central in Tolima and Cauca (Volcán Puracé) where it occurs from 2450-3100 m (Pyrz, 1999) (Fig. 17). It is locally sympatric with *M. germaniae* n. sp. (described below) at the highest reach of its altitudinal range. Specimens of *M. inderena* from extreme northern Ecuador on the eastern slopes of the Andes (Sucumbíos, Carchi) are considered

for the present as representing the nominate subspecies, although in general they are slightly larger, with a slightly broader pale VHW band, and generally reduced VHW ocelli, in some specimens approaching *M. i. fina*.

***Manerebia inderena antioquiensis* Pyrcz & Willmott n. ssp.**

Figs. 4A,B, 12B, 17

Manerebia inderena n. ssp. (Pyrcz, Willmott & Hall); Lamas & Viloria (2004: 215).

Diagnosis: This subspecies has yellow VHW bands, instead of white as in the nominate subspecies, and is typically smaller than the latter.

Description: MALE (Fig. 4A): *Head:* eyes, labial palpi and antennae same as in the nominate subspecies. *Thorax:* dorsal and ventral surface dark brown; legs paler brown. *Abdomen:* dorsal and ventral surface dark brown. *Wings:* forewing (length: 16.5-18.1 mm, mean: 17.3 mm, n=4) distal margin straight, apex rounded; hindwing rounded with very weakly pronounced notch at tornus. DFW medium brown; darker brown in discal area. DHW medium brown, slightly darker towards base, with two submarginal black ocelli ringed with dark orange in cells 1A-Cu2 and Cu2-Cu1. VFW ground colour medium brown, becoming slightly paler from base to apex; thin, straight, darker brown postdiscal line, parallel to distal margin, in cells 1A-R5; a tiny black submarginal spot ringed with dark orange in cell Cu2-Cu1; distinct, zigzag, darker brown submarginal line from tornus to apex; thin, straight, dark brown marginal line. VHW medium brown; pale yellowish postdiscal band from apex to tornus, passing through base of cell Cu1-M3; distinct, darker brown, strongly zigzag submarginal line; two small black submarginal ocelli, ringed with dark orange-brown, with white pupils, in cells 1A-Cu2 and Cu2-Cu1; thin, very faint, dark brown marginal line close to and parallel with distal margin. *Male genitalia* (Fig. 12B): similar to nominate subspecies.

FEMALE (Fig. 4B): Similar to male, except VHW postdiscal band whitish, instead of yellow, and ventral ocelli better marked.

Types: *Holotype male:* COLOMBIA: 1 male: Antioquia, San Felix, Las Antenas, 2700-3050 m, 13.IX.2003, T. Pyrcz leg., MZUJ; *Allotype female:* COLOMBIA: Antioquia, Medellín, El Retiro, Reserva San Sebastián, 2500-2800 m, 12.IX.2003, T. Pyrcz leg., TWP; *Paratypes (14 males):* COLOMBIA: 1 male: Antioquia, Medellín, El Retiro, Reserva San Sebastián, 2500-2800 m, 12.IX.2003, T. Pyrcz leg., TWP; 1 male: same locality, 2600m, 09.XI.2002, G. Rodríguez leg., TWP; 1 male: same locality, 2300-2800 m, 18-25.VII.2003, G. Rodríguez leg., TWP; 2 males: same locality, 2600-2800 m, 20.XII.2002, G. Rodríguez leg., (1 TWP, 1 BMNH); 1 male: same locality, 2600-2800 m, 26-30.VIII.2003, G. Rodríguez leg., TWP; 1 male: same locality, 2200-2600 m, 20.VIII.2003, G. Rodríguez leg., TWP; 2 males: Antioquia, Medellín, El Retiro, 2700m, 01.VIII.1993, J-F. Le Crom leg., TWP; 1 male: Antioquia, Polmifor, 24.VII.2001, G. Rodríguez leg., TWP; 1 male: Antioquia, Envigado, 2600-2800 m, 06.VI.2004, G. Rodríguez leg., TWP; 1 male: Antioquia, Los Llanos, vía a San Andrés km 10-14, 2600-2750 m, 14.XI.2003, T. Pyrcz leg., TWP; 2 males, Antioquia, El Retiro, 2600-2700 m, 18.XII.2001, G. Rodríguez leg., MBLI.

Etymology: This taxon is named after the Colombian department of Antioquia, where the type locality is situated.

Comments: To date this taxon is known only from the northern part of the Colombian Cordillera Central, from 2500-2800 m, where it appears to be locally not uncommon.

***Manerebia inderena fina* Pyrcz & Willmott, n. ssp.**

Figs. 4C,D, 12C, 17

Manerebia n. sp., n. ssp. (Pyrcz, Willmott & Hall); Lamas & Viloria (2004: 216, n. 1124b).

Diagnosis: This subspecies differs from other Ecuadorian sub-

species by having a narrower VHW postdiscal band. Along with *M. i. similis*, it may also be distinguished from all other subspecies by the dark, thin submarginal line on the VHW being more smoothly curving, rather than dentate as in other taxa. The nominate subspecies and *M. i. antioquiensis* also differ in having marked VHW submarginal ocelli, especially in 1A-Cu2 and Cu2-Cu1, that are usually absent or much reduced in *M. i. fina*. The width of the band in *M. i. fina* is about the same as in *M. germaniae germaniae*, which is locally sympatric, though generally occurring at higher elevations. The latter is distinguished externally with difficulty, by several subtle characters (see under *M. germaniae*). Another similar (though not sympatric) taxon is the Colombian *M. leaena lanassa*. Both *M. leaena* and *M. germaniae* are most reliably distinguished by the male genitalia, which have a curving uncus, relatively long subunci and 'teeth' at the dorsal edge of the valva near the base.

Description: MALE (Fig. 4C): *Head:* frons with a tuft of dark brown hair; eyes blackish-brown, smooth; labial palpi covered with blackish-brown hair; antennae dorsally chestnut, ventrally rufous, with white scales at the base of each segment, club dorsally slightly darker than shaft. *Thorax:* dorsal and ventral surface dark brown; legs paler yellowish-brown. *Abdomen:* dorsal and ventral surface dark brown. *Wings:* forewing (length: 18.5 mm, mean: 18.5 mm, n=2) distal margin almost straight, apex rounded; hindwing with distal margin rounded, with tornal notch almost absent. DFW medium brown, darker brown towards base. DHW medium brown. VFW ground colour medium brown, basal half slightly darker, bordered distally by very thin, indistinct, darker brown postdiscal line, that is slightly inclined towards apex, and curves slightly distally on approaching costa; faint, slightly wavy, darker brown submarginal line from tornus to apex; very thin, straight, dark brown marginal line. VHW medium brown; thin (c. 1.5 mm) very pale yellowish (almost white) postdiscal band from apex to tornus, very slightly concave, passing through base of cell Cu1-M3; faint darker brown submarginal line, smoothly curving from tornus to cell Cu1-M3, then slightly undulate to apex; white submarginal dots in cells Cu2-Cu1 and Cu1-M3; thin, dark brown marginal line close to and parallel with distal margin. *Male genitalia* (Fig. 12C): uncus curving slightly ventrally near middle, and bent more sharply near base, subunci of medium length; valvae thinning sharply at middle and tapering posteriorly, dorsally grooved, with 5-7 'teeth' at distal tip; aedeagus curving dorsally, with a couple of tiny 'teeth' on left hand side near middle.

FEMALE (Fig. 4D): Differs from male as follows: slightly larger (forewing length: 19 mm, n=1). Both wing surfaces paler brown. VHW postdiscal band wider.

Types: *Holotype male:* ECUADOR: Pichincha, Aloag-Tandapi rd., km 18, Sector Los Alpes, 2700-2750 m, 26.I.2004, T. Pyrcz & R. Garlacz leg., MZUJ; *Allotype female:* Pichincha, Volcán Pasochoa, nr. Amaguaña, 3500 m, 7.X.1997, K. Willmott leg., KWJH; *Paratypes (23 males):* ECUADOR: 4 males: Pichincha, Reserva Geobotánica Pululahua, 2300-2600 m, 11-12.II.2002, T. Pyrcz leg., TWP; 1 male: Pichincha, Chillo Gallo, San Juan-La Victoria, 3300-3400 m (unreliable), 30.I.2002, T. Pyrcz leg., TWP; 1 male: Pichincha, Volcán Pichincha, 3000-3050, X.2002, I. Aldas leg., TWP; 2 males: Pichincha, Aloag-Tandapi rd., 2800 m, II.2002, I. Aldas leg., TWP; 1 male: Pichincha, Nono - Nanegalito km 15/20, 2100 m, P. Boyer leg., MZUJ; 1 male: Pichincha, Volcán Pasochoa, 3000-3200 m, 07.X.1997, A. Neild leg., TWP; 1 male: Pichincha, Volcán Pasochoa, 2600-2700 m, 28.I.2002, T. Pyrcz leg., TWP; 5 males: Pichincha, Aloag-Tandapi rd., km 18, Sector Los Alpes, 2700-2750 m, 26.I.2004, T. Pyrcz & R. Garlacz leg., TWP; 1 male, same data, PB; 1 male, Pichincha, Nono-Nanegalito, 2700-3000 m, 10.V.1999, P. Boyer leg., PB; 1 male: Pichincha, environs de Nono, 2600m, 15.III.1998, P. Boyer leg., PB; 1 male: Pichincha, Nanegalito, 1800 m, IX.1996, P. Boyer leg., PB; 1 male: Pichincha, km 26 Nanegalito-Quito rd., Quebrada Molino, 2400 m, 16.X.1996, K. Willmott leg., KWJH; 1 male, Pichincha, km 7 Aloag-Tandapi rd., 2500 m, 13.VI.1994, J.

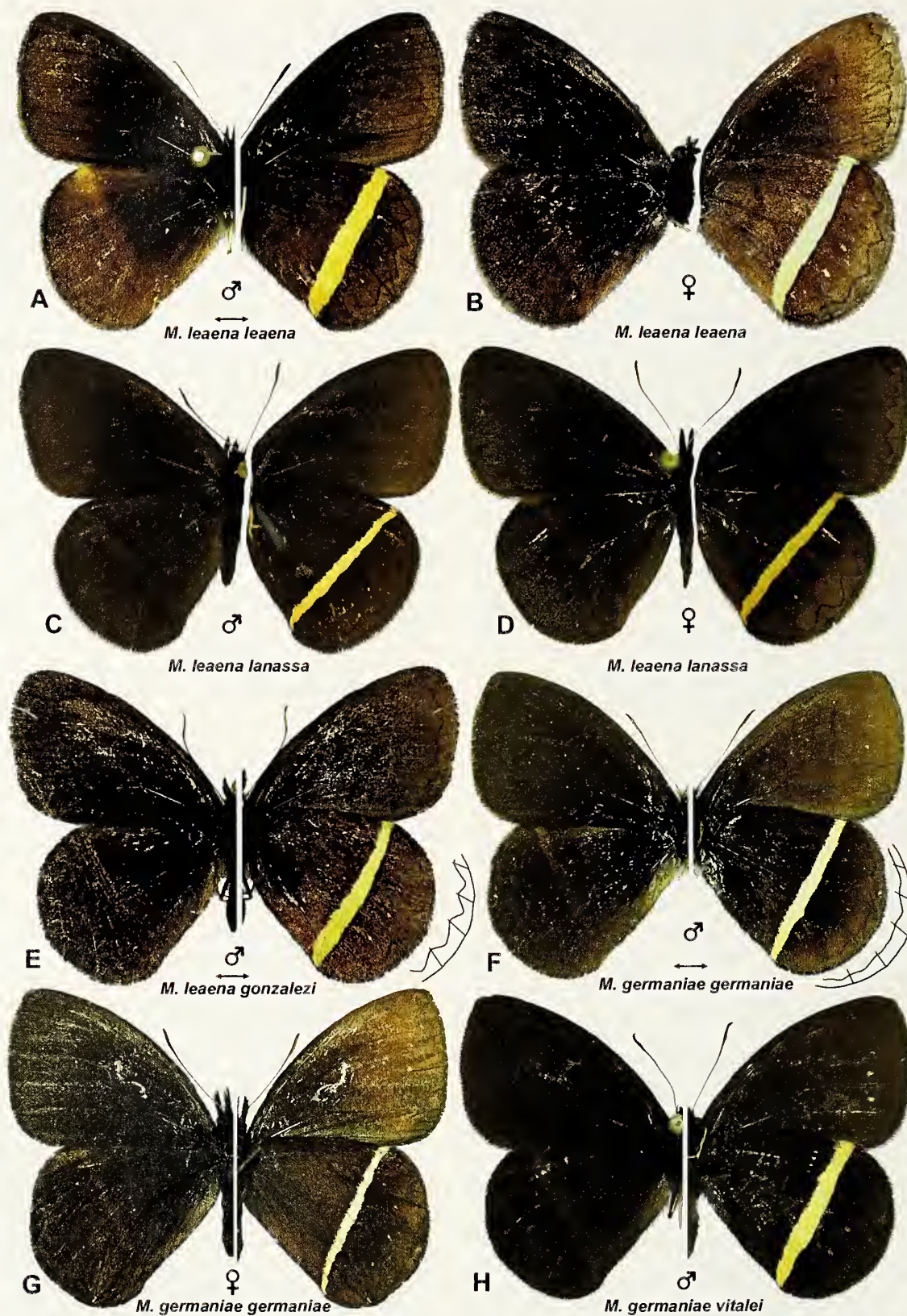


Fig. 1. Adult *Manerebia*, left dorsal view, right ventral view. Double arrows above names indicate image is reflected in vertical plane, so figured wings are righthand pair. A, *M. leaena leaena* male; B, *M. leaena leaena* female; C, *M. leaena lanassa* male; D, *M. leaena lanassa* female; E, *M. leaena gonzalezi* n. ssp. male; F, *M. germaniae germaniae* n. sp. male; G, *M. germaniae germaniae* n. sp. female; H, *M. germaniae vitalei* n. ssp. male. See Appendix 4 for specimen data.

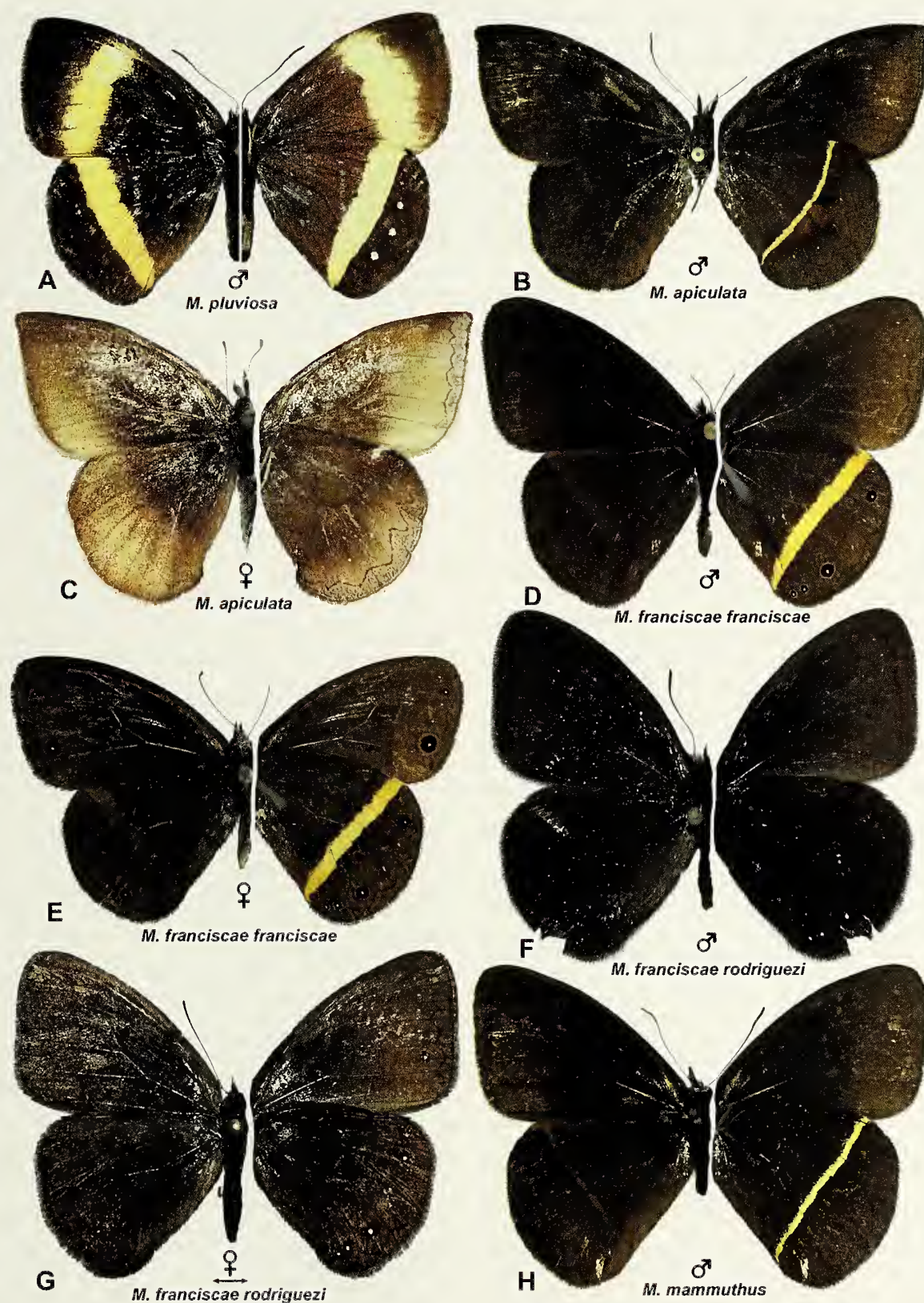


Fig. 2. Adult *Manerebia*, left dorsal view, right ventral view. Double arrows above names indicate image is reflected in vertical plane, so figured wings are righthand pair. A, *M. pluviosa* n. sp. male; B, *M. apiculata* male; C, *M. apiculata* female; D, *M. franciscae franciscae* male; E, *M. franciscae franciscae* female; F, *M. franciscae rodriguezi* n. ssp. male; G, *M. franciscae rodriguezi* n. ssp. female; H, *M. mammothus* n. sp. male. See Appendix 4 for specimen data.

Hall *leg.* MECN; **1 male**: Pichincha, km 5 Aloag-Tandapi rd., 2700m, 13.VI.1994, J. Hall *leg.* KWJH;

Etiymology: The name is the feminine form of the Latin adjective "finus", meaning narrow, with reference to the thin postdiscal band on the VHW.

Comments: This subspecies occurs on the western slopes of the Andes in northern Ecuador (Pichincha, Imbabura) and possibly also in southern Colombia (Nariño). It has been recorded from 2100-3200 m, and once at 3500 m (Volcán Pasochoa), though it is most common between 2200-2600 m. It is generally replaced at higher elevations by *M. germaniae*. Males are often encountered puddling along roads or streams, and are also attracted to rotting fish. We have also found males hilltopping on Loma La Palmira, flying low over the stunted bushes growing on the summit during bright sunlight, after 09:30 hrs.

***Manerebia inderena similis* Pyrcz & Willmott n. ssp.**

Figs. 4E,F, 12D, 17

Manerebia n. sp., n. ssp. (Pyrcz, Willmott & Hall); Lamas & Viloria (2004: 216, n. 1124c).

Diagnosis: This subspecies differs from the neighbouring *M. i. fina* to the north by the broader, pale VHW postdiscal band which is more strongly yellow especially towards anal margin. It is very similar to the east Andean *M. i. leaeniva*, but both west Andean subspecies (*M. i. similis* and *M. i. fina*) are distinguished from it and all others by the thin, dark submarginal line on the VHW being in most examined individuals more smoothly curving, rather than dentate.

Description: MALE (Fig. 4E): **Head**: eyes, labial palpi and antennae as in nominate subspecies. **Thorax**: dorsal and ventral surface dark brown; legs paler brown. **Abdomen**: dorsal and ventral surface dark brown. **Wings**: forewing (length: 19-20 mm; mean: 19.3 mm; n=3) distal margin almost straight, apex rounded; hindwing with distal margin rounded, with tornal notch almost absent. DFW medium brown, darker brown towards base. DHW medium brown. VFW ground colour medium brown, basal half slightly darker, bordered distally by very thin, indistinct, darker brown postdiscal line, that is slightly inclined towards apex and curves slightly distally on approaching costa; faint, slightly wavy, darker brown submarginal line from tornus to apex; very thin, straight, dark brown marginal line. VHW medium brown; broad (c. 2.5 mm) yellowish (more intense towards tornus) postdiscal band from apex to tornus, straight and of even width except tapering slightly at tornus, passing through base of cell Cu1-M3; faint, uneven darker brown submarginal line, more undulate in cells Cu2-Cu1 to M3-M2; white submarginal dots in cell Cu1-M3; tiny black submarginal ocellus, ringed with dark orange, with white pupil, in cell Cu2-Cu1, a black spot in anterior half of cell 1A-Cu2; thin, dark brown marginal line close to and parallel with distal margin. **Male genitalia** (Fig. 12D): uncus curving slightly ventrally near middle, and bent more sharply near base, subunci of medium length; valvae thinning sharply at middle and tapering posteriorly, dorsally grooved, with 5-7 'teeth' at distal tip; aedeagus curving dorsally, with a couple of tiny 'teeth' on left hand side near middle.

FEMALE (Fig. 4F): Similar to male but slightly paler brown ventrally.

Types: **Holotype male**: ECUADOR: Bolívar, Balzapamba, arriba de Santa Lucía, 2200-2250 m, 03.IX.2003, T. Pyrcz *leg.*, MZUJ; **Allotype female**: same data as the holotype, TWP; **Paratypes (34 males and 3 females)**: ECUADOR: **3 males**: Bolívar, Balzapamba, arriba de Santa Lucía, 2600-2650 m, 03.IX.2003, T. Pyrcz *leg.*, TWP; **12 males**: Bolívar, Balzapamba, arriba de Santa Lucía, 2200-2250 m, 03.IX.2003, T. Pyrcz *leg.*, TWP (11), BMNH (2); **5 males and 1 female**: Bolívar, Balzapamba, arriba de Santa Lucía, 2200-2250 m, 05.IX.2004, T. Pyrcz *leg.*, TWP; **1 male**: same locality and date, 2400-2450 m, T. Pyrcz *leg.*, TWP; **1 male**: same locality and date, 2500-2550 m, T. Pyrcz *leg.*, TWP; **2 males**: Bolívar, Balzapamba, Río

Alcacer, 2700m, 04.XI.1996, S. Attal *leg.*, MZUJ; **1 male**: Bolívar, old Guaranda road, VIII.1997, I. Aldas *leg.*, TWP; **3 males**: Cotopaxi, above Pilaló, 3000-3050 m, 03.IX.2004, T. Pyrcz *leg.*, TWP; **6 males and 2 females**: Azuay, Cuenca - Naranjal road, Molleturo, 2600-2650 m, 01.IX.2003, T. Pyrcz *leg.*, TWP.

Etiymology: The name is derived from the Latin "similis", meaning similar, with reference to this taxon's resemblance to the subspecies *M. i. leaeniva*, which occurs on the east slopes in central Ecuador.

Comments: This subspecies occurs in central western to south-western Ecuador, where it has been recorded above Pilaló (Cotopaxi), Santa Lucía (Bolívar) and on the western slopes of the Cajas massif near Molleturo (Azuay) from 2200-3000 m. In all these localities *M. i. similis* is the upper parapatric replacement of *M. undulata* n. sp.

***Manerebia inderena clara* Pyrcz & Willmott, n. ssp.**

Figs. 4G,H, 12E, 17

Manerebia n. sp., n. ssp. (Pyrcz, Willmott & Hall); Lamas & Viloria (2004: 216, n. 1124d).

Diagnosis: This subspecies differs from all others by the broad, pure whitish VHW postdiscal band, which is yellow in neighboring *M. i. leaeniva* to the south and yellowish posteriorly and tapering anteriorly in the similar *M. i. similis* from western Ecuador. The thin, dark submarginal line on the VHW is noticeably dentate, slightly more so than in *M. i. leaeniva* and noticeably more so than in *M. i. mirena*.

Description: MALE (Fig. 4G): **Head**: as in the nominate subspecies. **Thorax**: dorsal and ventral surface dark brown; legs paler brown. **Abdomen**: dorsal and ventral surface dark brown. **Wings**: forewing (length: 17.5-19 mm; mean: 18.2 mm; n=19) distal margin slightly convex, apex rounded; hindwing with distal margin slightly angled at vein M3, with tornal notch almost absent. DFW medium brown; darker brown in discal area. DHW medium brown, slightly darker towards base, with small black submarginal ocellus ringed with dark orange in cell Cu2-Cu1. VFW ground colour medium brown; thin, very indistinct, slightly curved, darker brown postdiscal line, in cells Cu2-M2; a minute white submarginal dot in cells Cu1-M3; indistinct, zigzag, darker brown submarginal line from tornus to apex; distal margin lined indistinctly with dark brown. VHW medium brown; whitish postdiscal band from apex to tornus, passing through base of cell Cu1-M3, straight and of even width, except tapering slightly in cell 1A-Cu2; faint, darker brown, strongly zigzag submarginal line; a small black submarginal ocellus, with a white pupil, faintly lined with dark orange, in cell Cu2-Cu1, with minute white submarginal dots in cells Cu1-M3 and M3-M2; distal margin lined indistinctly with dark brown. **Male genitalia** (Fig. 12E): uncus bent near base then flat, subunci of medium length; valvae thinning sharply at middle and tapering posteriorly, dorsally grooved, with 4-6 'teeth' at distal tip; aedeagus curving dorsally, with a couple of tiny 'teeth' on left hand side near middle.

FEMALE (Fig. 4H): Differs from male as follows: larger (forewing length 20.5 mm); ventral surface paler brown, with dark submarginal lines more distinct; a large ocellus in cell Cu2-Cu1 on VFW.

Types: **Holotype male**: ECUADOR: Napo, Baeza, Río Horituyacu [Oritoyacu], 1800 m, 08.VI.1999, T. Pyrcz & J. Wojtusiak *leg.* MZUJ; **Allotype female**: ECUADOR: Napo, Hda. San Isidro, 2000 m, 18.XII.1996, P. Boyer *leg.*, PB; **Paratypes (31 males)**: ECUADOR: **2 males**: same data as the holotype, TWP; **1 male**: Napo, Quito-Baeza rd., east of pass, 2300 m, 17.VI.1994, J. Hall *leg.*, KWJH; **1 male**: Napo, Baeza - Papallacta, 2100 m, 07.IV.1998, A. Neild *leg.*, TWP; **1 male**: Napo, SE of Cosanga, Río Chonta, 2000 m, 18.X.1996, K. Willmott *leg.*, KWJH; **1 male**: Napo, Baeza - Papallacta, 2100 m, 07.IV.1998, A. Neild *leg.*, TWP; **5 males**: Napo, Baeza area, 2050-2200 m, 02.X.1995, A. Neild *leg.*, TWP (4), MECN (1); **2 males**: Napo, Baeza, 2000-2200 m, 19.X.1996, A. Neild *leg.*, TWP; **7 males**: Napo, Baeza, 1800 m, IX.1996, P. Boyer *leg.*, TWP (5), BMNH (1), MZUJ

(1); **1 male**: Napo, Baeza, 1800 m, 10.XII.1996, P. Boyer *leg.*, TWP; **1 male**: Napo, San Isidro, 2000 m, 08.XII.1996, P. Boyer *leg.*, TWP; **1 male**: same data but 18.XII.1996, TWP; **1 male**: Napo, Cosanga, 1600 m, 06.XI.1996, P. Boyer *leg.*, PB; **1 male**: Napo, Baeza - Tena km 19, 2100 m, 04.XII.1997, P. Boyer *leg.*, TWP; **3 males**: Napo, Reserva Yanayacu, 2100-2150 m, 06-07.IX.2003, T. Pyrcz *leg.*, TWP; **3 males**: same locality, no date, H. Greeney *leg.*, MBLI.

Etymology: The name is derived from the Latin "clarus", meaning pale, with reference to the pale VHW postdiscal band.

Comments: *Manerebia inderena clara* has been recorded only in the Baeza area, in the valleys of the Ríos Papallacta and Cosanga, south to the Cordillera de los Huacamayos, from 1700-2400 m. It is not uncommon, and males can be found puddling along mountain streams in cloud forest, or feeding on horse dung or rotting fish.

Manerebia inderena leaeniva Pyrcz & Willmott, n. ssp.

Figs. 5C, 12F, 17

Manerebia n. sp., n. ssp. (Pyrcz, Willmott & Hall); Lamas & Viloria (2004: 216, n. 1124a).

Diagnosis: The yellow VHW band is twice as wide in this subspecies as in the nominate, and the VHW submarginal ocelli are reduced, similar to *M. i. fina*, *M. i. similis* and *M. i. clara*. In *M. i. clara* the VHW postdiscal band is as wide as in *M. i. leaeniva*, but white, while in *M. i. similis* from the west Andes it is as wide but a more intense yellow, and the VHW submarginal line is smoothly undulating rather than dentate. The southern subspecies *M. i. mirena* has a VFW ocellus in cell Cu2-Cu1, two to three ocelli in cells 1A-Cu2, Cu2-Cu1 on the VHW and an ocellus in cell Cu2-Cu1 on the DHW.

Description: MALE (Fig. 5C): **Head**: frons with a tuft of dark-brown hair; eyes blackish-brown; labial palpi covered with dark-brown hair; antennae dorsally pale brown, ventrally light beige, club laterally rufous, white scales at base of each segment. **Thorax**: dorsal and ventral surface dark brown; legs paler brown. **Abdomen**: dorsal and ventral surface dark brown. **Wings**: forewing (length: 17-20.5 mm; mean: 19 mm, n=11) distal margin slightly convex, apex rounded; hindwing with distal margin slightly angled at vein M3, with tornal notch almost absent. DFW medium brown; darker brown in discal area; androconial scales not apparent. DHW medium brown, slightly darker towards base, with two minute white submarginal dots in cells Cu2-Cu1 and Cu1-M3. VFW ground colour medium brown, becoming slightly paler from base to apex; thin, indistinct, slightly curved, darker brown postdiscal line, in cells Cu2-M2; a row of minute white submarginal dots in cells Cu2-Cu1 to M2-M1; indistinct, zigzag, darker brown submarginal line from tornus to apex; very thin, straight, dark brown marginal line. VHW medium brown; pale yellowish postdiscal band from apex to tornus, passing through base of cell Cu1-M3, straight and of even width; distinct, darker brown, strongly zigzag submarginal line; a small black submarginal ocellus, with a white pupil, in cell Cu2-Cu1; tiny white submarginal dots in cells Cu1-M1; thin, very faint, dark brown marginal line close to and parallel with distal margin. **Male genitalia** (Fig. 12F): uncus flat and bent near base, subunci of medium length; valvae thinning sharply at middle and tapering posteriorly, dorsally grooved, with 4-6 'teeth' at distal tip; aedeagus curving dorsally, with a couple of tiny 'teeth' on left hand side near middle.

FEMALE: Unknown.

Types: **Holotype male**: ECUADOR: Tungurahua, Chinchin, 2000 m, 06.II.2004, T. Pyrcz *leg.*, MZUJ; **Paratypes (15 males)**: ECUADOR: 2 males: Tungurahua, Río Verde Chico, 2100 m, 08.X.1995, A. Neild *leg.*, TWP; 2 males: same data as preceding but 24.IX.1995, TWP; 2 males: Tungurahua, Baños, Runtún, A. Jasiński *leg.*, TWP; 2 males: Tungurahua, Viscaya, 2100 m, 17.XI.1996, P. Boyer *leg.*, TWP; 5 males: Tungurahua, Triunfo - Patate, El Tablón, 3000m, P. Boyer *leg.*, TWP (2), PB (3); **1 male**: Tungurahua, Baños, El Tablón, 3000m, III.1999, I. Aldas *leg.*, MBLI; **1 male**: Tungurahua, Runtún,

2900-2950 m, 22.I.2002, J. Wojtusiak *leg.*, TWP.

Etymology: The subspecific name is derived from "leaena", the name of the species with which this taxon has been most often confused.

Comments: This subspecies is known from the upper valley of the Río Pastaza (Tungurahua) south to Morona-Santiago, where it has been recorded from 2100-3000 m, although it is more common in the lower part of this elevational range. Specimens from Morona-Santiago (Gualaceo-Limón road, vía Las Chacras, 2600-2850 m, TWP, KWJH) apparently represent this subspecies, but are excluded from the type series because we have been unable to examine sufficient material to reliably assess variation.

Manerebia inderena mirena Pyrcz & Willmott n. ssp.

Figs. 5A,B, 12G, 17

Diagnosis: This subspecies generally has a slightly wider VHW postdiscal band than *M. i. leaeniva*, a slightly more reddish brown ground colour, and prominent ocelli, in most individuals, in cell Cu2-Cu1 on the DHW and occasionally on the VFW and VHW in cell Cu2-Cu1. The uncus in *M. i. mirena* is usually more noticeably curved ventrally in the middle than in other subspecies, and the saccus is distinctive in always being swollen anteriorly.

Description: MALE (Fig. 5A): **Head**: frons with a tuft of dark brown hair; eyes blackish-brown, smooth; labial palpi covered with blackish-brown hair; antennae dorsally brown, ventrally dirty yellow, club slightly darker than shaft. **Thorax**: dorsal and ventral surface dark brown; legs yellowish-brown. **Abdomen**: dorsal and ventral surface dark brown. **Wings**: forewing (length: 18-19.5 mm; mean: 18.6 mm; n=3) distal margin slightly convex, apex rounded; hindwing with distal margin rounded, with tornal notch almost absent. DFW medium brown; darker brown in discal area. DHW medium brown, slightly darker towards base; a minute white submarginal dot in cell Cu1-M3, a small black ocellus ringed with dark orange with a white pupil in cell 1A-Cu2, a larger similar ocellus in cell Cu2-Cu1. VFW ground colour medium brown, becoming slightly paler from base to apex; thin, indistinct, straight, darker brown postdiscal line in cells Cu2-M2; a row of minute white submarginal dots in cells Cu2-Cu1 to M2-M1; in most individuals the dot in Cu2-Cu1 is replaced by a black ocellus, ringed with orange and with a white pupil, of variable size; indistinct, undulate, darker brown submarginal line from tornus to apex; very thin, straight, dark brown marginal line. VHW medium brown; a wide pale yellowish (more intense at tornus and costa) postdiscal band from apex to tornus, passing through base of cell Cu1-M3, straight and of even width; most individuals have one or two small black submarginal ocelli, with white pupils, in cell 1A-Cu2, and occasionally a larger ocellus in cell Cu2-Cu1, and white submarginal dots in other cells; darker brown, zigzag submarginal line; thin, dark brown marginal line close to and parallel with distal margin. **Male genitalia** (Fig. 12G): uncus curving slightly ventrally near middle, and bent more sharply near base, subunci of medium length; valvae thinning sharply at middle and tapering posteriorly, dorsally grooved, with 4-6 'teeth' at distal tip; aedeagus curving dorsally, with a couple of tiny 'teeth' on left hand side near middle.

FEMALE (Fig. 5B): Similar to male but paler with a fainter pattern on both dorsal and ventral wing surfaces.

Types: **Holotype male**: ECUADOR: Zamora-Chinchipe, Valladolid, Quebrada de los Muertos, 2550 m, XI.1999, I. Aldas *leg.*, MZUJ; **Allotype female**: ECUADOR: Loja, Loja-Zumbra, km 95-100, 2500-2600 m, 27.XI.1998, P. Boyer *leg.*, PB; **Paratypes (59 males and 1 female)**: ECUADOR: 2 males: Zamora-Chinchipe, Valladolid, no other data, P. Boyer *leg.*, PB; 2 males: Zamora-Chinchipe, km 34 Jimbura-San Andrés rd., 2900 m, 23.IX.1997, K. Willmott *leg.*, KWJH (1), MECN (1); 41 males: Zamora-Chinchipe, Valladolid, Quebrada de los Muertos, 2550 m, XI.1999, I. Aldas *leg.*, TWP (8), MBLI (33); 2 males: Zamora-Chinchipe, Loja - Zamora 2600m, 22.XI.1996, P. Boyer *leg.*, PB; 1 male: Loja, Loja-Zumbra, km 95-100,

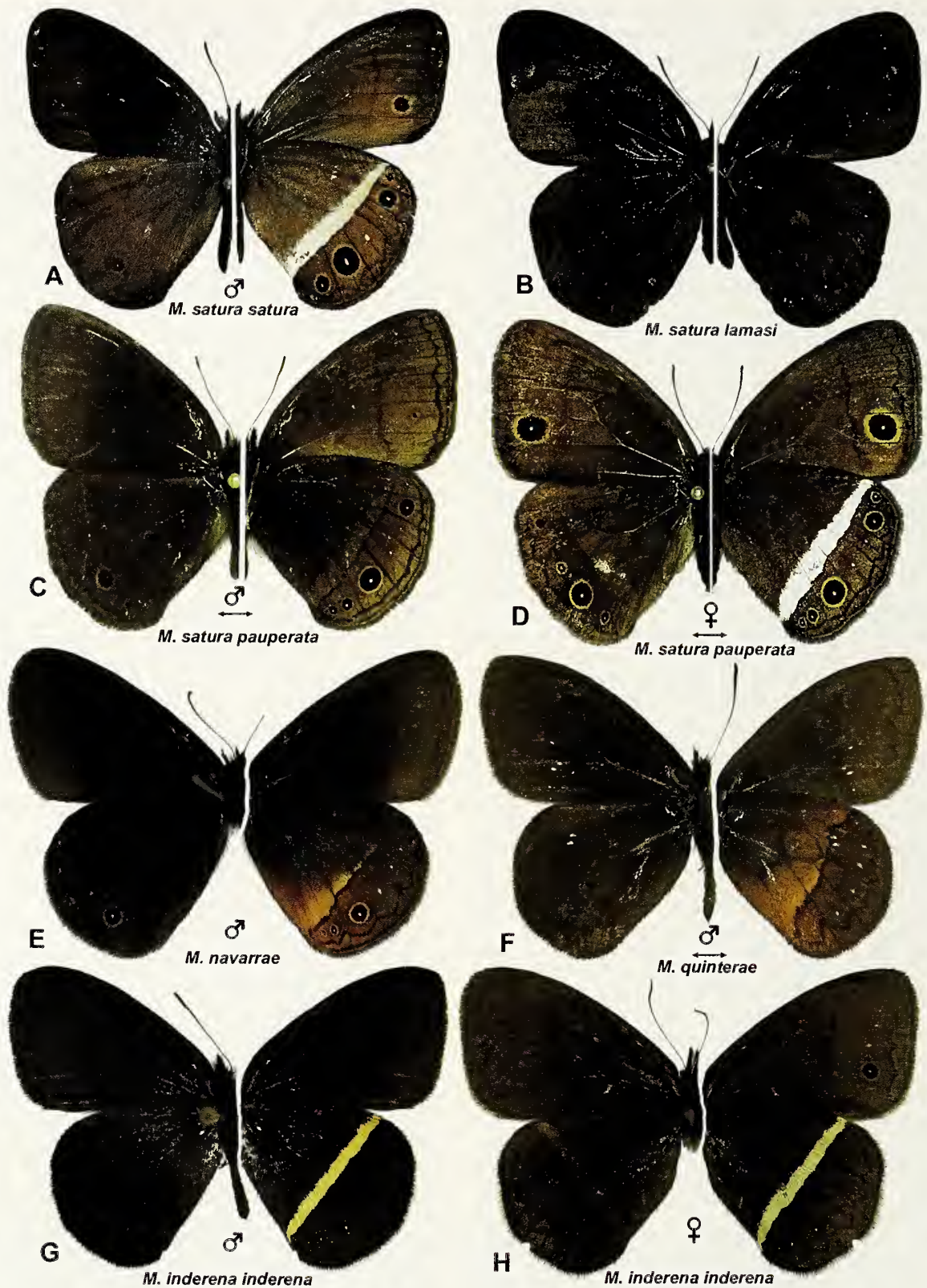


Fig. 3. Adult *Manerebia*, left dorsal view, right ventral view. Double arrows above names indicate image is reflected in vertical plane, so figured wings are righthand pair. A, *M. satura satura* male; B, *M. satura lamasi* n. ssp. male; C, *M. satura pauperata* n. ssp. male; D, *M. satura pauperata* n. ssp. female; E, *M. navarrae* male; F, *M. quinterae* male; G, *M. inderena inderena* male; H, *M. inderena inderena* female. See Appendix 4 for specimen data.

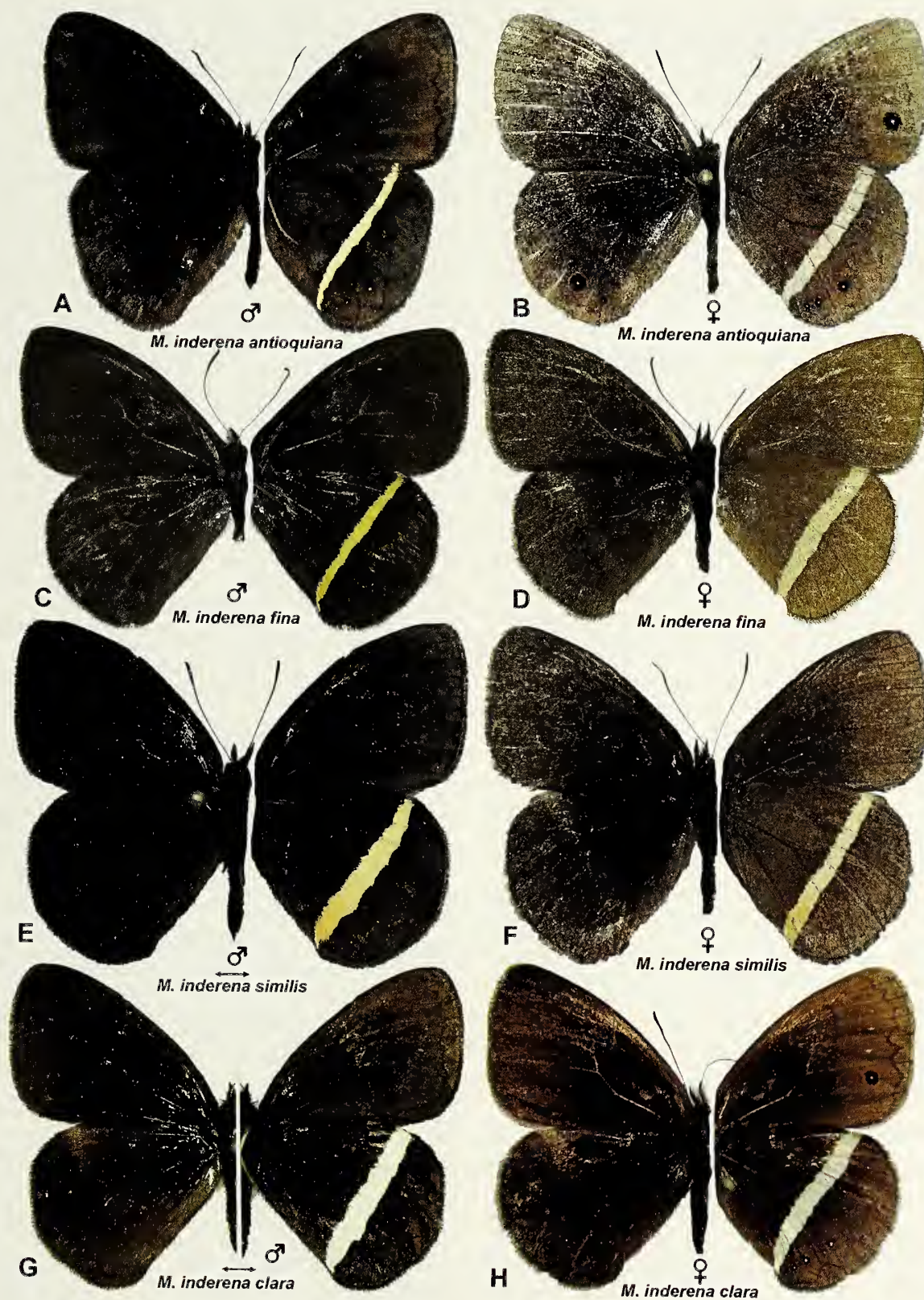


Fig. 4. Adult *Manerebia*, left dorsal view, right ventral view. Double arrows above names indicate image is reflected in vertical plane, so figured wings are righthand pair. A, *M. inderena antioquiiana* n. ssp. male; B, *M. inderena antioquiiana* n. ssp. female; C, *M. inderena fina* n. ssp. male; D, *M. inderena fina* n. ssp. female; E, *M. inderena similis* n. ssp. male; F, *M. inderena similis* n. ssp. female; G, *M. inderena clara* n. ssp. male; H, *M. inderena clara* n. ssp. female. See Appendix 4 for specimen data.

2500-2600m, 27.XI.1998, P. Boyer *leg.*, PB; **2 males**: Loja, Parque Nacional Podocarpus, Cajanuma, 2700m, 10.XI.1996, A. Neild, TWP; **1 male**: Loja, Loja-Zamora, El Basurero, 2600m, 22.XI.1997, P. Boyer *leg.*, PB; **2 males**: Loja, Old road Loja - Zamora, 2800 m, XI.1999, I. Aldas *leg.*, MBLI; **4 males, 1 female**: same data as preceding but 2500 m, MBLI; **1 male**: Loja, Cenén Alto, 2800m, XI.1999, I. Aldas *leg.*, MBLI. PERU: **1 male**: Cajamarca, Tabaconas, I. Aldas *leg.*, TWP.

Etymology: The name "mirena" is composed from the subspecific names "milaena" and "inderena".

Comments: This species occurs from southeastern Ecuador on both slopes of the Andes (Zamora-Chinchi, Loja) to north-eastern Peru (Tabaconas). It has been recorded in cloud forest within a narrow elevational band, from 2500-3000 m, where it may, however, be locally common.

Manerebia golondrina Pyrcz & Willmott n. sp.

Figs. 5D, 12H, 17

Manerebia n. sp. (Pyrcz, Willmott & Hall); Lamas & Viloria (2004: 216, n. 1128).

Diagnosis: This species lacks the pale VHW postdiscal band that occurs in other *Manerebia* species with similar genitalia (*M. inderena*, *M. prattorum* n. sp.). The wing shape, ocelli on the VHW and ocellus on the DHW in cell Cu2-Cu1 are somewhat similar to *M. inderena*. The male genitalia are indistinguishable from those of *M. inderena*, except for lacking lateral 'teeth' on the aedeagus as present in *M. inderena*, a character that varies within other species.

Description: MALE (Fig. 5D): **Head**: frons with a tuft of long, dark brown hair; eyes glabrous, dark brown; labial palpi covered with black and brown hair ventrally and dorsally, laterally with short black and light brown scales, last segment covered with light brown scales and ventrally with short brown hair; antennae brown with white scales at the base of each segment, club only slightly thicker than shaft. **Thorax**: dorsal and ventral surface dark brown; legs paler brown. **Abdomen**: dorsal and ventral surface dark brown. **Wings**: forewing (length: 19-21 mm, mean: 20.1 mm, n=10) distal margin slightly convex, apex rounded; hindwing with distal margin slightly angled at vein M3, with tornal notch almost absent. DFW medium brown; darker brown in discal area, androconial scales not apparent. DHW medium brown, with small black submarginal ocellus ringed with dark orange in cell Cu2-Cu1. VFW ground colour medium brown, darker brown in basal half; very indistinct, darker brown postdiscal line, in cells Cu2-Cu1 to costa; indistinct, slightly undulate, darker brown submarginal line from tornus to apex; distal margin lined indistinctly with dark brown. VHW medium brown, darker towards base; slightly paler brown, thin, straight postdiscal line from apex to tornus; faint, darker brown, undulate submarginal line; a black submarginal ocellus, ringed with dark orange, with a white pupil, in cell Cu2-Cu1, a similar but smaller ocellus in the anterior half of cell 1A-Cu2, and a black dot in the posterior half of the same cell; distal margin lined indistinctly with dark brown. **Male genitalia** (Fig. 12H): uncus bent near base then flat, subunci of medium length; valvae thinning sharply at middle and tapering posteriorly, dorsally grooved, with 4-6 'teeth' at distal tip; aedeagus curving dorsally, laterally smooth.

FEMALE: Unknown.

Types: **Holotype male**: ECUADOR: Carchi, Reserva Forestal Las Golondrinas, 2350 m, 20.V.1999, T. Pyrcz & J. Wojtusiak *leg.* MZUJ; **Paratypes (29 males)**: ECUADOR: **1 male**: same data as the holotype but 2600m, 22.VI.1999, TWP; **3 males**: same data but 2200 m, 22.VI.1999, TWP; **2 males**: same data but 2150 m, 23.VI.1999, TWP; **3 males**: same data but 2000 m, 23.VI.1999, TWP; **1 male**: same data but 2550 m, 02.VII.1999, TWP; **1 male**: same data but 2300 m, 23.VI.1999, TWP; **1 male**: same data but 2200 m, 22.VI.1999, TWP; **1 male**: same data but 27.VI.1999, TWP; **1 male**: same data but 2150 m, 24.VI.1999, BMNH; **2 males**: Carchi, nr. La Carolina, Reserva Las Golondrinas, Santa Rosa, 1700 m, 05.IX.1996, K. Will-

mott *leg.*, KWJH; **1 male**: Carchi, Tulcán - Maldonado, 1300-1600 m, 24.V.1997, A. Jasiński *leg.*, TWP; **1 male**: Carchi, Tulcán-Maldonado km 40 a 50, 2800-3200 m, P. Boyer *leg.*, PB; **2 males**: same locality, 2450 m, 27.VIII.2004, T. Pyrcz *leg.*, TWP; **9 males**: Imbabura, La Carolina, Route de Buenos Aires km 25, 2600m, 05.V.2000, P. Boyer *leg.*, PB (7), TWP (2).

Etymology: The specific name is derived from the name of the private cloud forest reserve where most of the individuals, including the holotype, were collected, the Reserva Las Golondrinas, managed by Fundación Golondrinas.

Comments: This species is most closely related to *M. inderena*, with which it is currently not known to be sympatric. We treat it as a distinct species because it occurs at notably lower elevations than *M. inderena fina*, and because of the phenotypic similarity of *M. inderena fina* and *M. inderena inderena* from northeastern and western Ecuador. In addition, specimens of *M. inderena fina* are known from Cotacachi at 3000m, approximately 40 km south of the nearest locality of *M. golondrina*, between which there are no obvious geographical barriers. This species is known to date only from northwestern Ecuador (Fig. 17), an area that is a local centre of endemism for cloud forest satyrines (e.g., *Lasiophila phalaesia alce* Pyrcz, *Corades violacea* Pyrcz, *Pedaliodes phrasica immaculata* Pyrcz). It is found on the south (Buenos Aires) and north (Las Golondrinas) banks of the Río Mira. It should certainly also occur in southwestern Colombia south of the Río Nariño valley. The two males collected by KRW were both attracted to rotting fish. Other individuals were collected in traps baited with excrement. *Manerebia golondrina* occurs in middle elevation cloud forests from 1600-2600 m, but sampling with baited traps carried out by the first author in the Reserva Las Golondrinas, along an elevational transect, indicated the species to occur most commonly from 2000 to 2600m.

Manerebia prattorum Pyrcz & Willmott n. sp.

Figs. 5E, 12I, 17

Manerebia n. sp. (Pyrcz, Willmott & Hall); Lamas & Viloria (2004: 216, n. 1129).

Diagnosis: This species is easily distinguished from its congeners in the northern Andes by the postdiscal orange band on the DHW only. The only species with somewhat similar pattern is *Manerebia lisa* (Weymer), occurring in central Peru, but in that taxon the band is darker, with blurred edges, narrowing gradually from anal to costal margin. The male genitalia of *M. lisa* show that the two species are not closely related, however, being similar to *M. satura* (see characters grouping *M. satura* with *M. franciscæ*, under the latter species). The size and wing shape of *M. prattorum* are similar to *M. inderena mirena* n. ssp. and *M. undulata milaena* n. sp. n. ssp. *Manerebia prattorum*, however, lacks the ventral magenta or greyish sheen in the distal marginal areas that characterises *M. undulata*, and does not have the DHW submarginal ocelli that occur in *M. inderena mirena*. The male genitalia differ from *M. inderena* and *M. undulata* in having only 2-3 'teeth' at the distal tip of the valva, and from *M. rufanalis* in having a straighter uncus and differently shaped valva (see diagnosis of the latter species).

Description: MALE (Fig. 5E): **Head**: frons with a tuft of short, brown hair; eyes chocolate brown, smooth; labial palpi covered with short, medium brown hair; antennae medium brown, slightly lighter on ventral surface. **Thorax**: dorsal and ventral surface dark brown; legs paler brown. **Abdomen**: dorsal and ventral surface dark brown. **Wings**: forewing (length: 17-17.5 mm; mean: 17.2 mm, n=4) distal margin almost straight, apex rounded; hindwing with distal margin slightly angled at vein M3, tornal notch almost absent. DFW medium brown, darker brown towards base. DHW ground colour medium brown; a broad, orange postdiscal band extending from costa to anterior half of cell 1A-Cu2, basal edge straight, distal edge kinked at vein M3, so that widest point of band is at vein M3. VFW ground colour medium brown, basal half slightly darker, bordered distally by very thin, indistinct, darker brown postdiscal line, that

is slightly inclined towards apex; faint, slightly wavy, darker brown submarginal line from tornus to apex. VHW medium brown; broad whitish postdiscal band from apex to tornus, tapering towards costa and tornus and widest in cells Cu2-Cu1 and Cu1-M3, passing through base of cell Cu1-M3; faint, slightly undulate darker brown submarginal line. **Male genitalia** (Fig. 121): uncus nearly straight except where bent sharply near base, subunci of medium length; valvae thinning sharply at middle and tapering posteriorly, dorsally grooved, with 2-3 'teeth' at distal tip; aedeagus curving dorsally.

FEMALE: Unknown.

Types: *Holotype male:* PERU: Piura, arriba de Canchaque, 2100 m, 0522/7934, 05.VI.2000, G. Lamas *leg.*, MUSM; *Paratypes* (10 males): PERU: 2 males: same data as the holotype, MUSM; 2 males: same data as the holotype except R. Robbins *leg.*, USNM; 1 male: same data as preceding except 07.VI.2000, USNM; 1 male: same data as preceding except G. Lamas *leg.*, MUSM; 4 males: West slopes of Andes, N. Peru, 10 000 ft., June 1912, Pratt, Joicey Bequest, Brit. Mus. 1934-120, BMNH.

Etymology: This species is dedicated to Antwerp Edgar Pratt and his son Felix Pratt, who first collected it almost a century ago.

Comments: *Manerebia prattorum* occurs at 2100-2600 m on the western slopes of the Andes in northwestern Peru, on the west slopes of the Andes, east of the locality of Canchaque and possibly in the valley of Huancabamba (Piura). Specimens potentially representing another undescribed subspecies have also been collected in northwestern Peru (Cajamarca), west of Chiclayo, above the locality of La Florida (Fig. 17).

Manerebia trimaculata (Hewitson, 1870)

Figs. 5F,G,H, 13A, 18

Lymanopoda trimaculata Hewitson (1870: 159). **TL:** Ecuador, Morona-Santiago, St. Rosario. **ST male:** BMNH(T) [examined].

Manerebia trimaculata (Hewitson); Lamas & Viloria (2004: 216).

Diagnosis: *Manerebia trimaculata* and the related species, *M. undulata* n. sp. and *M. interrupta*, are all characterised by a light greyish or magenta marginal sheen along the distal quarter of the ventral surface of both wings, and a thin, dark brown, undulate line passing through the center of the VHW discal cell. The male genitalia (Fig. 13A) of all three species are distinctive in the uncus being almost straight, so that the dorsal edge of the tegumen and uncus form a smoothly curving line, the subunci are very short and the valva is sharply constricted in the middle to produce the attenuated distal half. This species might arguably be considered conspecific with the west Andean *M. undulata*, but our reasons for keeping them separate are discussed under that species. The VHW yellow band in specimens of the syntypic series is reduced to three spots near the tornus (Fig. 5F), but in other specimens it can be fully developed, but rather irregular at the basal edge (Fig. 5G). *Manerebia trimaculata* is readily distinguished from other similar species by the two or more well developed submarginal ocelli in cells Cu2-Cu1 and Cu1-M3 on the DHW, and usually by the submarginal ocellus in cell Cu2-Cu1 on the VFW. Some specimens of *M. interrupta* have similar but smaller ocelli and are typically smaller in size.

Comments: This species is confined to southeastern Ecuador (Morona-Santiago and Zamora-Chinchiipe) (Fig. 18), where it is rather uncommon, and it was omitted entirely by Brown (1944). *Manerebia trimaculata* occurs in relatively intact cloud forests from 2500-2800 m, and in contrast to the closely related *M. interrupta*, it frequents openings within the forest, rarely straying into cleared areas. A single specimen was collected in the Cordillera del Cóndor on the border between Ecuador and Peru (Camp Achupalla, 15 km E. Gualaquiza, 2100-2200 m, MUSM).

Manerebia undulata Pyrcz & Hall, n. sp.

Manerebia undulata is characterised by a thin, dark

brown, undulate line passing through the center of the VHW discal cell, a character only otherwise occurring distinctly and consistently in *M. interrupta* and *M. trimaculata*. Also distinctive is the paler brown or purplish shading around the distal margin of the VHW and apical area of the VFW (also occurring in *M. trimaculata* and *M. interrupta*), and the markedly undulate dark brown VHW submarginal line. The first two of these characters distinguish *M. undulata* from most other west Ecuadorian species (*M. inderena*, *M. germaniae*, *M. ignilineata*). The last two characters also occur in *M. rufanalis* n. sp., but that has distinct male genitalia, with a smoothly arching uncus (not straight), longer subunci and a smooth ventral edge to the valva, which gradually tapers posteriorly. The most closely related species, as indicated by wing pattern and the male genitalia (see discussion under *M. trimaculata*), seem to be *M. interrupta* and *M. trimaculata*. The former occurs at higher elevations and in drier habitats on the western slopes and may be distinguished by its smaller size, the more pointed forewing apex, DHW submarginal ocelli, and uneven VHW postdiscal band (in forms with a full band). *Manerebia undulata* is not known to be sympatric with the eastern slope *M. trimaculata*, with which it might be considered conspecific, but given that *M. undulata* is much commoner at substantially lower elevations, not (or only exceptionally) polymorphic in expression of the hindwing band, and lacks prominent ocelli on the DHW in any subspecies, we treat the two taxa as distinct species.

Unlike *M. trimaculata* and *M. interrupta*, polymorphism of the pale VHW postdiscal band in *M. undulata* is rare or absent (but see discussion under *M. u. undulata*). Two subspecies are recognised.

Manerebia undulata undulata Pyrcz & Hall, (n. sp.)

Figs. 6A,B,C, 13B, 18

Manerebia n. sp. (Pyrcz, Willmott & Hall); Lamas & Viloria (2004: 216, n. 1125).

Diagnosis: The nominate subspecies has narrower, although somewhat variable, pale VHW postdiscal bands and is slightly larger than *M. undulata milaena* (described below).

Description: **MALE** (Fig. 6A): **Head:** frons with a tuft of brown hair; eyes dark brown, smooth; labial palpi covered with brown hair; antennae dorsally greyish-brown, ventrally orangeish, with whitish scales at base of each segment, tip darker brown. **Thorax:** dorsal and ventral surface dark brown; legs paler brown. **Abdomen:** dorsal and ventral surface dark brown. **Wings:** forewing (length: 17.5-19 mm; mean: 18 mm; n=12) distal margin slightly convex, apex rounded; hindwing with distal margin slightly angled at vein M3, with tornal notch almost absent. DFW medium brown, darker brown in basal half. DHW medium brown, slightly darker towards base; minute black submarginal ocellus with white pupil in cell Cu2-Cu1. VFW ground colour medium brown, slightly darker towards base; thin, distinct, almost straight, darker brown postdiscal line from anal margin to near costa; distinct, undulate, darker brown submarginal line from tornus to apex; very thin, indistinct, dark

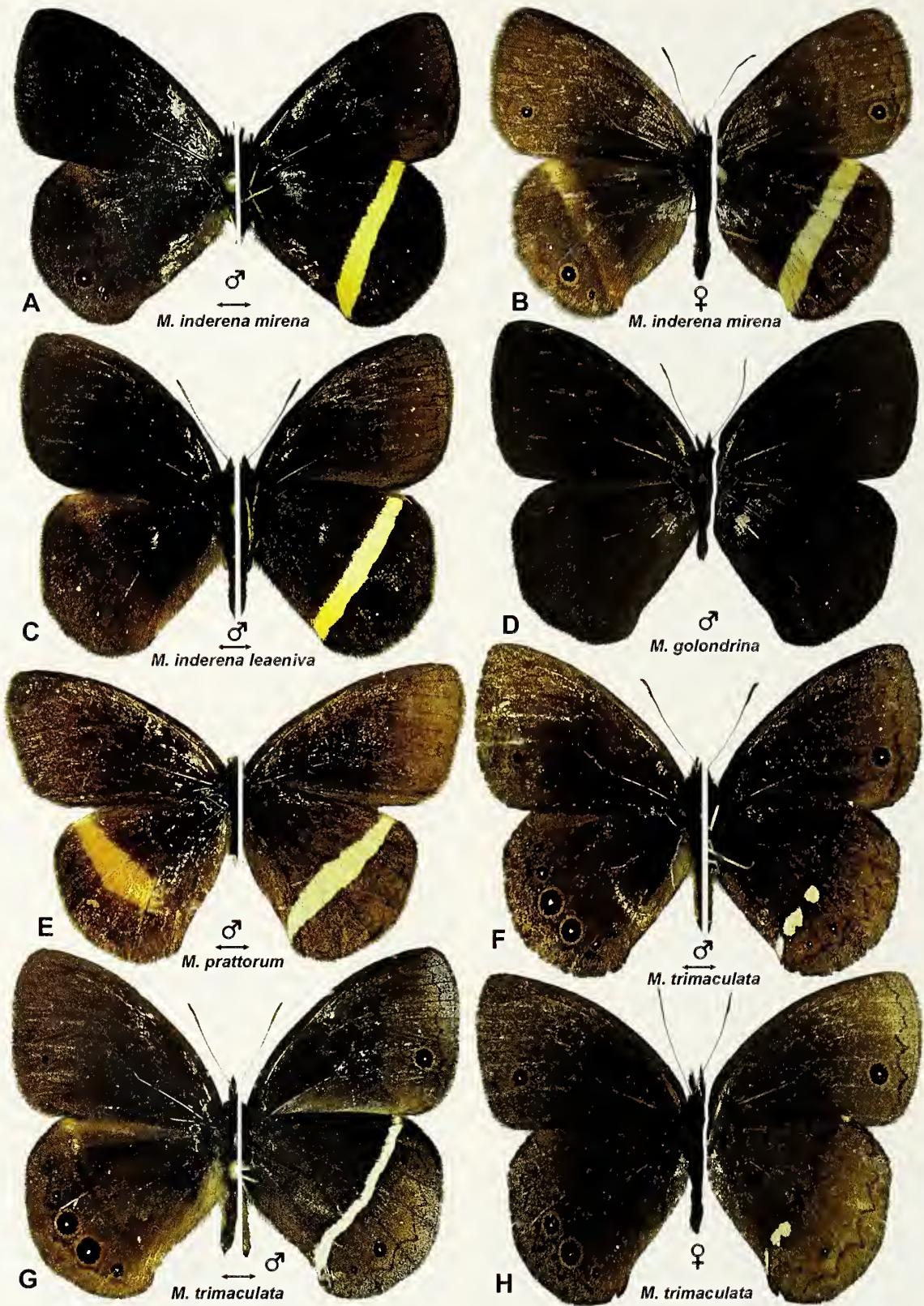


Fig. 5. Adult *Manerebia*, left dorsal view, right ventral view. Double arrows above names indicate image is reflected in vertical plane, so figured wings are righthand pair. A, *M. inderena mirena* n. ssp. male; B, *M. inderena mirena* n. ssp. female; C, *M. inderena leaeniva* n. ssp. male; D, *M. golondrina* n. sp. male; E, *M. prattorum* n. sp. male; F, *M. trimaculata* male (form); G, *M. trimaculata* male (form); H, *M. trimaculata* female. See Appendix 4 for specimen data.

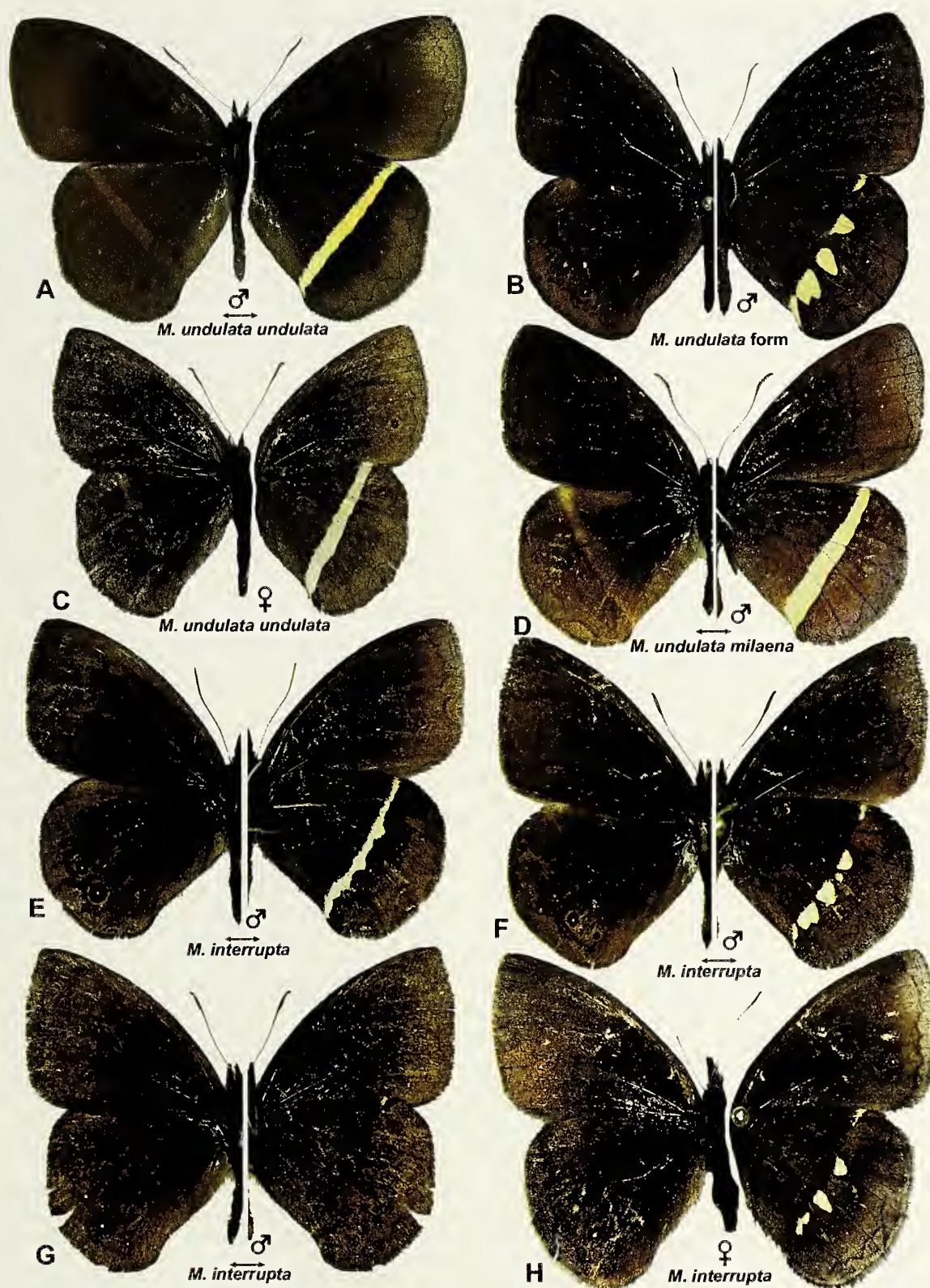


Fig. 6. Adult *Manerebia*, left dorsal view, right ventral view. Double arrows above names indicate image is reflected in vertical plane, so figured wings are righthand pair. A, *M. undulata undulata* n. sp. male; B, *M. undulata undulata* ? male; C, *M. undulata undulata* n. sp. female; D, *M. undulata milaena* n. ssp. male; E, *M. interrupta* male (form); F, *M. interrupta* male (form); G, *M. interrupta* male (form); H, *M. interrupta* female. See Appendix 4 for specimen data.

brown marginal line; pale brownish scaling extending in from distal margin to surround dark brown submarginal line, from cell Cu1-M3 to apex. VHW medium brown; indistinct, undulating dark brown line from costa to anal margin through middle of discal cell; thin, whitish postdiscal band from apex to tornus, passing through base of cell Cu1-M3, slightly convex and thinning slightly towards costa; darker brown, strongly zigzag submarginal line; minute black submarginal ocelli, with white pupils, in cell 1A-Cu2 (two) and cell Cu2-Cu1, white submarginal dots in cells Cu1-M3 and M3-M2; pale brownish scaling extending in from distal margin to surround dark brown submarginal line from tornus to apex; very faint, thin, dark brown marginal line close to and parallel with distal margin. **Male genitalia** (Fig. 13B): uncus straight, with dorsal edge and dorsal edge of tegumen forming a smooth curve, subunci short; valvae thinning sharply at middle and tapering posteriorly, dorsally grooved, with 4-6 'teeth' at distal tip; aedeagus curving dorsally, laterally smooth.

FEMALE (Fig. 6C): Differs from male as follows: ventral surface lighter and duller; an ocellus in cell 1A-Cu2 on the forewing.

Types: *Holotype* male: ECUADOR: Bolívar, Balzapamba, arriba de Santa Lucía, 1700-1750 m, 03.IX.2003, T. Pyrcz leg., MZUJ; *Al-lotype* female: same data as the holotype, MZUJ; *Paratypes* (55 males and 2 females): ECUADOR: 31 males and 1 female: same data as the holotype, TWP (29), BMNH (2 males); 2 males: Bolívar, Balzapamba, arriba de Santa Lucía, 1400-1450 m, 03.IX.2003, T. Pyrcz leg., TWP; 2 males: same locality, 1600-1650 m, 05.IX.2004, T. Pyrcz leg., TWP; 9 males: Loja, Zambí, 2200-2300 m, 08.III.1998, P. Boyer leg., TWP (4), PB (5); 2 males: Loja, Guayquichuma, 28.V.1996, S. Attal & I. Aldas leg., TWP; 1 male: same data but 21.V.1996, TWP; 4 males: Loja, Guayquichuma, 1800-2000 m, 15.IV.1997, A. Jasiński leg., TWP (3), MHNUC (1); 1 male: Zamora - Chinchipe, Zambí, A. Jasiński leg., TWP; 3 males: Cotopaxi, Pilaló, 2500-3000 m, VII.1996, I. Aldas leg., TWP; 1 male: Pichincha, Aloag-Sto. Domingo rd., Tandapi, 1550 m, 10.VIII.1993, J. Hall leg., MECN; 2 males: same data as preceding except 1700 m, 3.VIII.1996, K. Willmott leg., KWJH; 1 male: Pichincha, old Quito-Sto. Domingo rd., nr. Chiriboga, Río Las Palmeras, 1900 m, 14.VIII.1993, J. Hall leg., KWJH; 1 female: Loja, Zambí, P. Boyer leg., PB.

Etymology: The name is the feminine form of the Latin adjective "undulatus", meaning undulate, in reference to the undulate VHW submarginal line.

Comments: We have examined two specimens of *M. undulata* in the TWP recently collected by Stéphane Attal in southwestern Ecuador (Loja) and labelled "Yangana, route de Valladolid, 2600m, 23.V.2000" which have a broken pale VHW postdiscal band (Fig. 6B). A single male in the BMNH from "Ecuador" is similar. These specimens are associated with *M. undulata* rather than *M. interrupta* on the basis of their larger size (30% larger than *M. interrupta*) and rounded forewing apex. It is possible that these specimens represent a local population in which the broken band is monomorphic, given the lack of known specimens with a complete hindwing band from this area and phenotypic stability of the species elsewhere, but more material is required to confirm this.

The nominate subspecies occurs on the western and southwestern slopes of the Ecuadorian Andes, where it may be locally common. It has been recorded from 1400-2300 m.

Manerebia undulata milaena Pyrcz & Willmott, n. ssp.

Figs. 6D, 13C, 18

Manerebia n. sp., n. ssp. (Pyrcz, Willmott & Hall); Lamas & Vilorio (2004: 216, n. 1125b).

Diagnosis: This subspecies is smaller than the nominate. The VHW pale postdiscal bands are wider, and broaden from the costa to tornus. The ventral distal marginal sheen is wider and a purplish, rather than pale brown, colour. The dorsal surface ground colour is also paler, so that the VHW postdiscal band is faintly visible. The male genitalia do not differ consistently from

M. undulata undulata.

Description: MALE (Fig. 6D): **Head:** eyes, labial palpi and antennae as in the nominate subspecies. **Thorax:** dorsal and ventral surface dark brown; legs paler brown. **Abdomen:** dorsal and ventral surface dark brown. **Wings:** forewing (length: 17-18.5 mm; mean: 17.1 mm, n=3) distal margin angled slightly at vein M1, apex rounded; hindwing outer margin almost perfectly rounded with a very slight angle at vein M3, and a slight tornal notch; fringes light brown. DFW medium brown, darker brown in basal half, androconial scales not apparent; a faint, darker, undulate submarginal line. DHW medium brown, slightly darker towards base; very faint, postdiscal band of pale scales reflecting VHW band, stronger at costa; slightly paler yellowish brown, sparse scales in marginal area; darker, zigzag submarginal line. VFW ground colour medium brown, darker towards base; thin, distinct, almost straight, darker brown postdiscal line from anal margin to near costa; distinct, slightly undulate, darker brown submarginal line from tornus to apex; very thin, indistinct, dark brown marginal line; pale purplish grey scaling extending in from distal margin to surround dark brown submarginal line, from cell Cu1-M3 to apex; row of tiny white submarginal dots in cells Cu2-Cu1 to M2-M1. VHW medium brown; indistinct, undulating dark brown line from costa to anal margin through middle of discal cell; thin, yellowish white postdiscal band from apex to tornus, passing through base of cell Cu1-M3, approximately straight and broadening continuously from costa to tornus; darker brown, strongly zigzag submarginal line; pale purplish grey scaling extending in from distal margin to surround dark brown submarginal line from tornus to cell M1-Rs. **Male genitalia** (Fig. 13C): uncus straight, with dorsal edge and dorsal edge of tegumen forming a smooth curve, subunci short; valvae thinning sharply at middle and tapering posteriorly, dorsally grooved, with 4-6 'teeth' at distal tip; aedeagus curving dorsally, laterally smooth.

FEMALE: Unknown.

Types: *Holotype* male: ECUADOR: Loja, Cordillera de Lagunillas, Jimbura - Laguna Negra, 3000-3200 m, 15.V.1998, A. Jasiński leg., MZUJ; *Paratypes:* 2 males: same data as the holotype, TWP.

Etymology: The name is a composite of the names of two other related Ecuadorian *Manerebia* taxa: (*M. inderena*) *mirena* and (*M. inderena*) *leaniva*.

Comments: Unlike *M. undulata undulata*, which is a cloud forest species of intermediate elevations, the type series of *M. undulata milaena* was collected at the tree-line in the Cordillera de Lagunillas range, at 3000-3200 m. Unfortunately, there is virtually no natural vegetation remaining in southwestern Ecuador below 2800m, so it may be impossible to locate the true natural lower elevational limit. A single individual of (apparently) *M. undulata milaena* (in the MUSM), collected further south on the west slopes of the Andes in Peru, east of Chiclayo (Cajamarca), at 2400-2600 m, is excluded from the type series. Specimens of *M. prattorum* from the same locality (see southernmost data point on Fig. 17) represent a subspecies different from that in southern Ecuador, and the same might apply to *M. undulata*.

Manerebia interrupta (Brown, 1944)

Figs. 6E,F,G, H, 13D, 18

Penrosada apiculata form *interrupta* Brown (1944: 257, male genit. Fig. 1618). **TL:** Ecuador, Azuay, Seville de Oro. **HT male:** Ecuador, Azuay, Seville de Oro, 2500 m, 15.II.[19]39. AME [photograph examined].

= *Manerebia keradialenka* Hayward (1968: 205, figs. 4, 8). **TL:** Ecuador, Azuay, Tarquí. **HT male:** Ecuador, Azuay, Tarquí, 08.V.[19]65, Luis Peña leg. IMLT [examined].

Penrosada apiculata form *curvilinea* (Weymer); Brown (1944: 258) (misidentification).

Manerebia interrupta (Brown); Lamas & Vilorio (2004: 215).

Diagnosis: As in *M. trimaculata*, the VHW yellow band is variably expressed, and varies from complete absence (Fig. 6G), through

a series of semicircular spots (Fig. 6F), to being complete, with an uneven distal edge (Fig. 6E). *Manerebia interrupta* is much smaller than *M. trimaculata*, has a more acute forewing apex, and lacks an ocellus on the VFW in cell Cu1-Cu2. Brown (1944), and presumably earlier workers, misidentified this species in Ecuador as the superficially similar but genitally distinct Colombian *M. apiculata*, and named a form with the band broken into spots as form *interrupta*. Hayward (1968) subsequently named a form without any hindwing band as *Manerebia keradialeuka*. Brown's name *interrupta* thus becomes the first available name for this species, to which *M. keradialeuka* Hayward is a junior synonym (Lamas & Viloria, 2004). Male genitalia as illustrated (Fig. 13D).

Comments: *Manerebia interrupta* appears to be most closely related to *M. undulata* and *M. trimaculata* (see discussion under those species). Although it has not been reported from the same sites as either *M. trimaculata* or *M. undulata*, its closest relatives, it appears to replace each locally at higher elevations and in drier habitats. This species occurs from south-central (Morona-Santiago: Gualaceo-Chiguinda rd.; Gualaceo-Limón road.) to southern Ecuador (Loja: above Catamayo; Cerro Palma, Loja-Zamora rd.) and in northern Peru (Piura: entre Las Minas y El Tambo) on the western slopes of the Andes. It occurs from 2400 m up to the tree-line around 3200 m. Males were found flying low to the ground in areas of recent bamboo regrowth on landslips in elfin forest/páramo mosaic, and also in a dry river gulley through desert scrub on the southwestern slopes. The species is most commonly encountered in drier habitats, such as those of the inter-Andean valleys. We have also observed males hilltopping at Cerro Palma, and occasionally puddling at damp sand. The species appears to be highly seasonal; whereas it was very common along the Gualaceo-Limón road in February (wet season), no individuals were observed in the same locality in August, during the dry season.

Manerebia rufanalis Pyrcz & Hall, n. sp.

This species is distinguished from all others by the rusty suffusion and submarginal ocelli at the tornus of the DHW. The light magenta sheen along the distal margins on the ventral surface, especially at forewing apex and on the hindwing, is also distinctive. The VFW ocellus in cell Cu1-Cu2 is generally, but not always, well developed and is occasionally also apparent in adjacent cells. The VHW yellow band is variable and appears to be relatively wider in smaller specimens. The genitalia are distinctive within the genus, and differ from those of *M. inderena* and *M. undulata* by having an arched uncus and relatively long subunci, similar to species such as *M. leaena* and *M. satura*, while the elongate valva, which lacks 'teeth' at the dorsal edge near the base, similar to *M. inderena* and *M. trimaculata*, has a smoothly upwardly curving (rather than "stepped") basal edge. In addition, the valva always has relatively few (usually 2-3) large 'teeth' at the distal tip.

Manerebia rufanalis rufanalis Pyrcz & Hall, (n. sp.)

Figs. 7A, B, 13E, 19

Manerebia n. sp. (Pyrcz, Willmott & Hall); Lamas & Viloria (2004: 216, n. 1126).

Diagnosis: The nominate subspecies is distinguished from *M. r. fernandina* as discussed below. There is some variation in this taxon,

and some individuals have an additional ocellus on the DHW in cell Cu1-M3.

Description: MALE (Figs. 7A): **Head:** frons with a tuft of dark brown hair; eyes chocolate brown, smooth; labial palpi covered with dark brown hair; antennae dorsally chestnut, ventrally rufous, with white scales at the base of each segment, club same colour as shaft. **Thorax:** dorsal and ventral surface dark brown; legs paler brown. **Abdomen:** dorsal and ventral surface dark brown. **Wings:** forewing (length: 18-21 mm; mean: 19.9 mm; n=8) distal margin slightly angled at vein M2, apex rounded; hindwing slightly angled at vein M3, with slight tornal notch. DFW medium brown, darker brown in basal half. DHW medium brown, slightly darker towards base; a small submarginal black ocellus ringed with orange, with a white pupil, in anterior half of cell 1A-Cu2, a larger similar ocellus in cell Cu2-Cu1; orange-brown scaling along the anal margin, broadening into tornus to extend to edge of ocellus in cell 1A-Cu2. VFW ground colour medium brown, darker in basal half; thin, very faint, straight, darker brown postdiscal line in cells Cu2-M1; black submarginal ocellus ringed with dark yellow, with a white pupil, in cell Cu2-Cu1; three white submarginal dots in cells Cu1-M3 to M2-M1; indistinct, undulate, darker brown submarginal line from tornus to apex; thin, very faint, dark brown marginal line; pale greyish scaling extending from distal margin to surround dark brown submarginal line in cells M3-M2 to costa. VHW medium brown, scattered with very sparse red-brown scales in basal two-thirds, denser along anal margin and costa, particularly at apex; pale yellow postdiscal band (becoming white at basal edge) from apex to tornus, passing through base of cell Cu1-M3, straight and of even width; faint, darker brown, zigzag submarginal line; three small black submarginal ocelli, with a white pupil, in cells 1A-Cu2 and Cu2-Cu1; a white submarginal dot in cell Cu1-M3; thin, dark brown marginal border; pale greyish scaling sparsely extending in from distal margin to just past dark brown submarginal line from tornus to cell M3-M2. **Male genitalia** (Fig. 13E): uncus smoothly arching, subunci relatively long; basal edge of valvae smoothly curving, dorsally grooved, with 2-3 'teeth' at distal tip; aedeagus thin and shallowly curving dorsally, laterally smooth.

FEMALE (Fig. 7B): Similar to male but lighter on both wing surfaces.

Types: **Holotype male:** ECUADOR: Tungurahua, Baños, Runtún, 2600-3000 m, 06.VIII.1998, T. Pyrcz leg., MZUJ; **Allotype female:** ECUADOR: Loja, Old road Loja-Zamora, 2600m, XI.1999, I. Aldas, leg., MBLI; **Paratypes** (32 males and 1 female): ECUADOR: 1 male: Tungurahua, Baños, TWP; 1 male: Tungurahua, Baños, V.1995, I. Aldas leg., TWP; 1 male: Tungurahua, Runtún, 3000m, 21.XI.1998, P. Boyer leg., PB; 1 male: Tungurahua, Baños-Puyo rd., Río Machay, 1700 m, 19-20.VIII.1993, J. Hall leg., MECN; 1 male: same data as preceding except 12.IX.1993, KWJH; 1 male: Napo, Baeza, 1800 m, IX.1996, P. Boyer leg., PB; 1 male: Zamora-Chinchipe, San Andrés, 2200 m, 13.VIII.1998, T. Pyrcz leg., TWP; 1 male: Zamora-Chinchipe, región de Valladolid, 2500 m, 25.XI.1993, B. Méry & S. Attal leg., TWP; 1 male: Zamora-Chinchipe, Río San Francisco, 1400[?] m, 11.XI.1989, A. Crosson-du-Cormier & S. Attal leg., TWP; 1 male: Zamora-Chinchipe, San Andrés - Calderón, 2200-2600 m, 20.V.1998, A. Jasiński leg., TWP; 1 male: Zamora-Chinchipe, nr. Valladolid, Quebrada Tapichalaca, 1950 m, 4.XI.1997, K. Willmott leg., KWJH; 1 male: Zamora-Chinchipe, km 34 Jimbura-San Andrés rd., 2900 m, 23.IX.1997, K. Willmott leg., KWJH; 1 male: Zamora-Chinchipe, Zamora-Loja rd., nr. Sabanillas, Quebrada San Ramón, 1700 m, 27-29.X.1997, K. Willmott leg., KWJH; 13 males: Zamora-Chinchipe, Valladolid, Quebrada de los Muertos, 2550 m, XI.1999, I. Aldas leg., TWP (4), MBLI (9); 3 males: Loja, Old road Loja-Zamora, 2500-2600m, XI-XII.1999, I. Aldas leg., MBLI; 1 male: Tungurahua, El Tablón, 3000m, III.1999, I. Aldas leg., MBLI; 1 male: Tungurahua, Baños, Río Verde, 2300 m, III.1999, G. Velástegui leg., MBLI; 1 female: Loja, Old road Loja-Zamora, 2600m, XI.1999, I. Aldas, leg., MBLI, PERU: 1 male: Cajamarca, Tabaconas, VIII.1996,

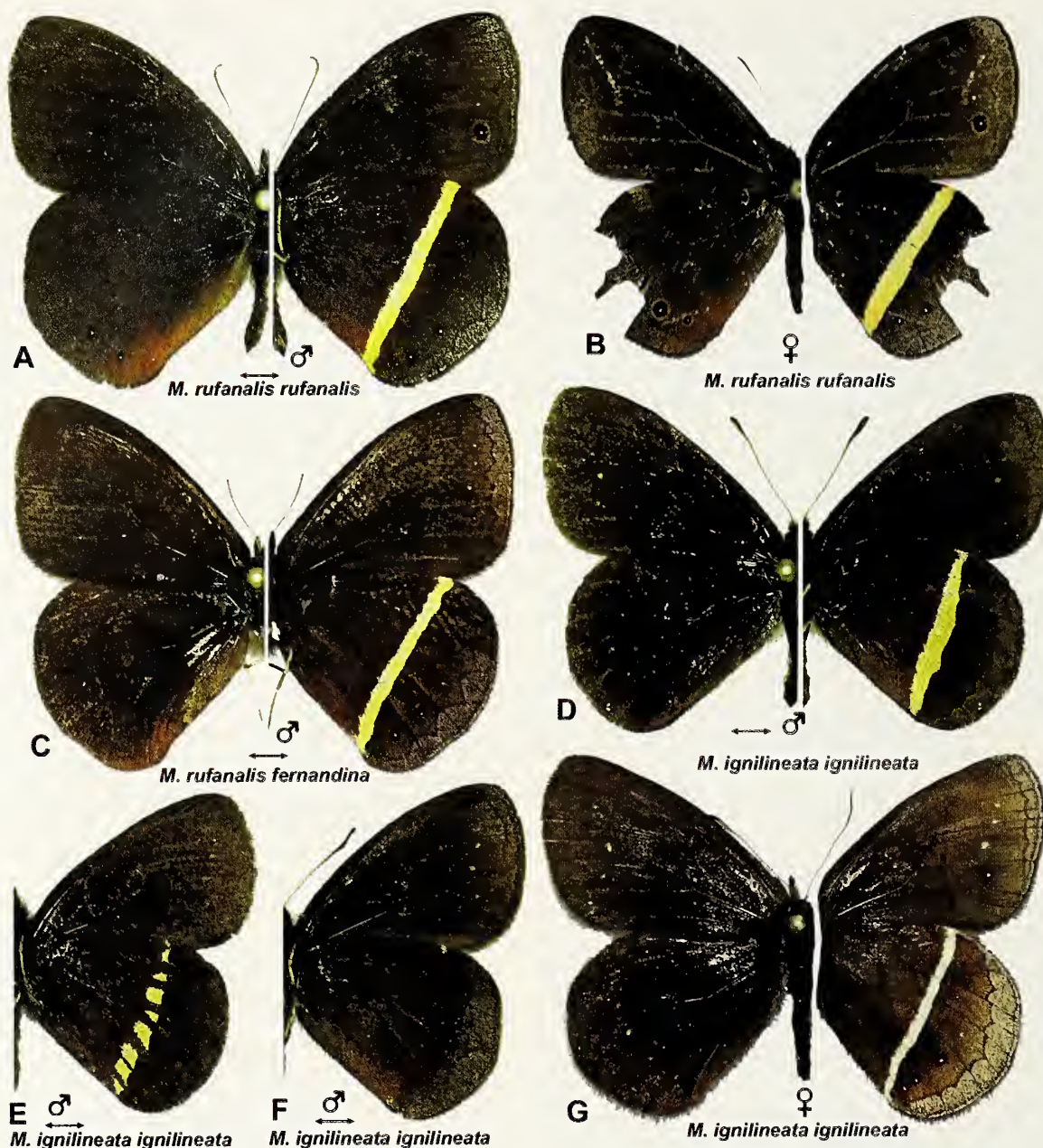


Fig. 7. Adult *Manerebia*, left dorsal view, right ventral view. Double arrows above names indicate image is reflected in vertical plane, so figured wings are righthand pair. A, *M. rufanalis rufanalis* n. sp. male; B, *M. rufanalis rufanalis* n. sp. female; C, *M. rufanalis fernandina* n. ssp. male; D, *M. ignilineata ignilineata* male (form); E, *M. ignilineata ignilineata* male (form); F, *M. ignilineata ignilineata* male (form); G, *M. ignilineata ignilineata* female. See Appendix 4 for specimen data.

I. Aldas leg., TWP.

Etymology: The species name is derived from the Latin "rufus", reddish brown, referring to the distinctive color in the anal area of the DHW.

Comments: This subspecies is known from the east Andean slopes in central Ecuador to far northern Peru, and it is one of the most common *Manerebia*, occurring in fairly intact cloud forest habitats from 1700-2900 m. Males may often be encountered puddling at stream and river banks, particularly at urine, and are attracted to rotting fish. We have also observed males hilltopping

on open, grassy summits with low bushes, along the Jimbura-San Andrés road.

***Manerebia rufanalis fernandina* Pycz & Willmott, n. ssp.**

Figs. 7C, 13F, 19

Manerebia n. sp., n. ssp. (Pycz, Willmott & Hall); Lamas & Viloria (2004: 216, n. 1126b).

Diagnosis: This subspecies is slightly smaller than the nominate,

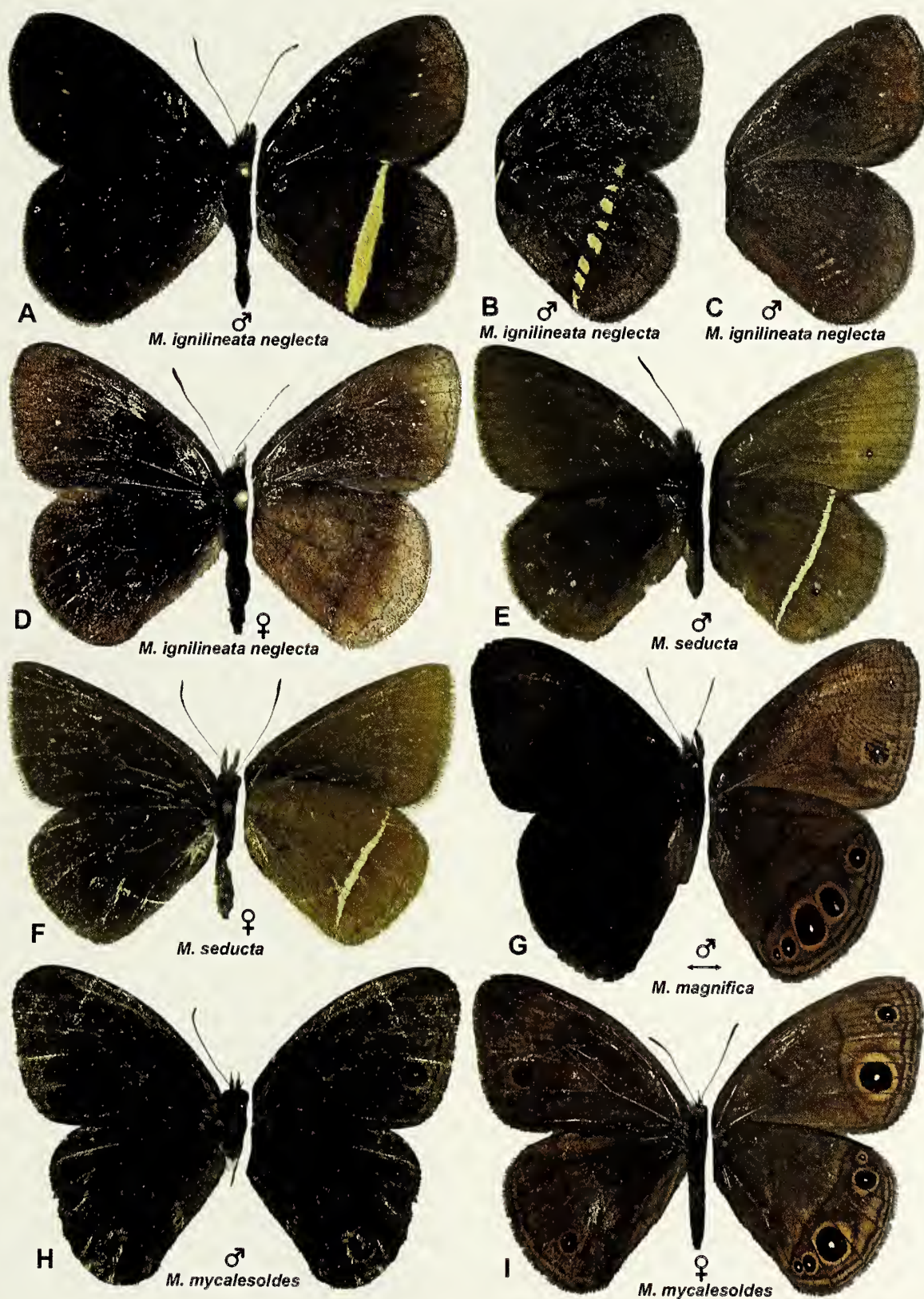


Fig. 8. Adult *Manerebia*, left dorsal view, right ventral view. Double arrows above names indicate image is reflected in vertical plane, so figured wings are righthand pair. A, *M. ignilineata neglecta* male (form); B, *M. ignilineata neglecta* male (form); C, *M. ignilineata neglecta* male (form); D, *M. ignilineata neglecta* male (form); E, *M. seducta* n. sp. male; F, *M. seducta* n. sp. female; G, *M. magnifica* n. sp. male; H, *M. mycalesoides* male; I, *M. mycalesoides* female. See Appendix 4 for specimen data.

has reduced reddish-brown scaling on the DHW anal area and the ocelli are smaller on both wing surfaces.

Description: MALE (Fig. 7C): **Head:** frons with a tuft of dark brown hair; eyes chocolate brown, smooth; labial palpi covered with long, dark brown hair; antennae dorsally chestnut, ventrally orange, with white scales at the base of each segment, club same colour as shaft. **Thorax:** dorsal and ventral surface dark brown; legs paler brown. **Abdomen:** dorsal and ventral surface dark brown. **Wings:** forewing (length: 18 mm, mean: 18 mm, n=1) distal margin slightly angled at vein M2, apex rounded; hindwing slightly angled at vein M3, with slight tornal notch. DFW medium brown, darker brown in basal half. DHW medium brown, slightly darker towards base; two small submarginal black ocelli ringed with orange, with white pupils, in anterior half of cell 1A-Cu2 and in cell Cu2-Cu1; orange-brown scaling in the tornus, not extending to ocellus in 1A-Cu2. VFW ground colour medium brown, darker in basal half; thin, very faint, straight, darker brown postdiscal line in cells Cu2-M1; small black submarginal ocellus ringed with dark orange, with a white pupil, in cell Cu2-Cu1; three white submarginal dots in cells Cu1-M3 to M2-M1; distinct, undulate, darker brown submarginal line from tornus to apex; thin, very faint, darker brown marginal line; pale purplish grey scaling extending from distal margin to surround dark brown submarginal line in cells Cu2-Cu1 to costa. VHW medium brown, scattered with very sparse red-brown scales in basal two-thirds; pale yellow postdiscal band (becoming white at basal edge) from apex to tornus, passing through base of cell Cu1-M3, slightly concave and of even width; faint, darker brown, zigzag submarginal line; two small black submarginal ocelli, with a white pupil, in anterior half of cell 1A-Cu2 and in Cu2-Cu1; a white submarginal dot in cell Cu1-M3; thin, dark brown marginal border; pale purplish grey scaling sparsely extending in from distal margin to just past dark brown submarginal line from tornus to cell M3-M2. **Male genitalia** (Fig. 13F): uncus smoothly arching, subunci relatively long; basal edge of valvae smoothly curving, dorsally grooved, with a single "tooth" at distal tip; aedeagus thin and shallowly curving dorsally, laterally smooth.

FEMALE: Unknown.

Types: **Holotype male:** ECUADOR: Azuay, Girón, San Fernando, 2500 m, 08.V.1998, P. Król *leg.*, MZUJ; **Paratypes: 2 males:** same data as the holotype, TWP.

Etymology: The name is derived from that of the type locality, San Fernando.

Comments: The three types of *M. rufanalis fernandina* are the only known specimens of this species from the western Andes. The type locality of *fernandina* (San Fernando) is in the Cuenca valley, an area of endemism in cloud forest satyrids, generally at the subspecific level (e.g., *Lasiophila phalaesia kroli* Pyrcz, *Pedaliodes xanthosphenisca* ssp. Pyrcz, in prep.). Since a number of other east Andean cloud forest taxa cross over to the western slopes in southern Ecuador (Willmott & Hall, in prep.), this taxon may also occur further south, where little habitat remains at a suitable elevation.

Manerebia ignilineata (Dognin, 1896)

This is the smallest species of *Manerebia*, and is easily distinguished from all other species by the elongate, rounded wings (a character shared with *M. pervaga*), the irregular VHW submarginal line placed relatively far from the distal margin, and the male genitalia. The latter are markedly distinct from all other north Andean species, except *M. seducta*, in the short, squat valva, which is enlarged in the basal half, lacks a dorsal groove, has very large, sparse distal 'teeth', and whose tips flare outwards in ventral view.

Like *M. trimaculata* and *M. interrupta*, this species is polymorphic in the expression of the VHW postdiscal band, and occurs in three fairly discrete forms; one form has a fully developed VHW band (Fig. 7D), the second has the band broken into a row of quadrate spots by dark brown lines on the veins (Fig. 7E), and the last has the band completely absent (Fig. 7F).

Manerebia ignilineata ignilineata (Dognin, 1896)

Figs. 7D, E, F, G, 14A, 20

Lymanopoda ignilineata Dognin (1896: 134). **TL:** Ecuador, Loja, Loja. **HT male:** Ecuador, Loja, Environs de Loja, 1890. BMNH [examined]

Penrosada ignilineata (Dognin); D'Abrera (1988: 824).

Manerebia ignilineata (Dognin); Lamas & Viloria (2004: 215) (in part).

Diagnosis: The nominate subspecies differs from *M. i. neglecta* as discussed under that taxon. The expression of the VHW pale postdiscal band is polymorphic in both sexes (Figs. 7D, E, F, G). Male genitalia as illustrated (Fig. 14A).

Comments: Dognin's (1896) description of this species is concise but clear, and the holotype male, which has an indistinct, broken VHW postdiscal band intermediate between the specimens figured in Figs. 7E and 7F, is in the BMNH. *Manerebia ignilineata ignilineata* occurs at the cloud forest/páramo ecotone, and in the lower páramo, in southern Ecuador (Morona-Santiago: Gualaceo-Limón; Loja: Jimbura-San Andrés rd.; Loja-Zamora rd.) on the eastern, and in far south, western slopes of the Andes, from 2700–3300 m. The species seems to be very local and seasonal. Males fly usually 1–3 m above dense stands of bamboo growing in páramo intermixed with elfin forest. *Manerebia ignilineata* occurs also in northern Peru, east of the Río Marañón, as a distinct subspecies, *M. ignilineata jalca* Pyrcz (2004).

Manerebia ignilineata neglecta (Brown, 1944), **n. stat.**

Figs. 8A, B, C, D, 14B, 20

Penrosada lanassa form *neglecta* Brown (1944: 260, male genit. fig. 1619). **TL:** Ecuador, Tungurahua, Minza Chica. **HT male:** Ecuador, Tungurahua, Minza Chica, 08.IV.[19]39, 3200 m, *leg.* F. M. Brown, No. B1619. AME [photograph examined], **n. stat.**

= *Penrosada lanassa* form *discontinua* Brown (1944: 260, male genit. fig. 1617). **TL:** Ecuador, Tungurahua, Minza Chica. **HT male:** Ecuador, Tungurahua, Minza Chica, 08.IV.[19]39, 3200 m, *leg.* F. M. Brown, No. B1617. AME [photograph examined].

[*Penrosada lanassa* (C. & R. Felder); Brown (1944: 258)]

Manerebia ignilineata (Dognin); Lamas & Viloria (2004: 215) (in part).

Diagnosis: This subspecies differs from the nominate in the forewing distal margin being nearly straight, except angled slightly at vein M2, instead of convex, and in the hindwing being slightly angled between M1 and M2 and at M3, instead of almost perfectly rounded. It also lacks the shining magenta colour on the distal margin of the VHW and apex of the VFW, and the VHW submarginal line is more zigzag than in the nominate.

Redescription: MALE (Figs. 8A, B, C): **Head:** frons with sparse blackish hair; eyes blackish-brown, smooth; labial palpi covered with black hair; antennae dorsally brown, ventrally dirty yellow, club formed of 10–11 segments, twice width of shaft. **Thorax:** dorsally blackish-brown, ventrally medium brown. **Abdomen:** dorsally blackish-brown, laterally and ventrally medium-brown. **Wings:** forewing distal margin nearly straight except angled slightly at vein M2, apex rounded; hindwing slightly angled between M1 and M2 and at M3, tornal notch absent. Fringes of both fore and hindwings light-brown. DFW medium brown, darker towards base. DHW almost uniform medium brown, except for faint trace of postdiscal band

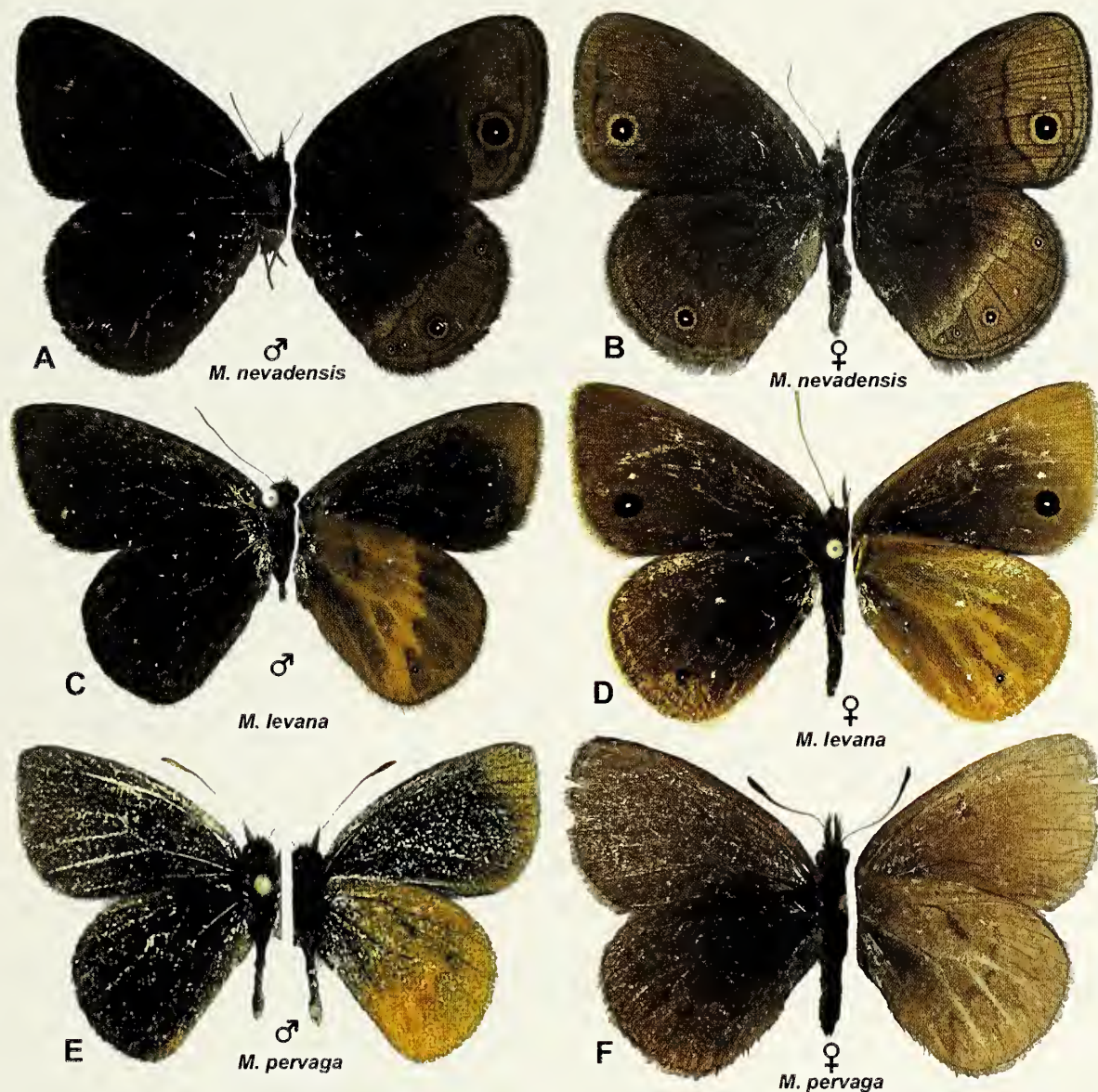


Fig. 9. Adult *Manerebia*, left dorsal view, right ventral view. Double arrows above names indicate image is reflected in vertical plane, so figured wings are righthand pair. A, *M. nevadensis* male; B, *M. nevadensis* female; C, *M. levana* male; D, *M. levana* female; E, *M. pervaga* n. sp. male; F, *M. pervaga* n. sp. female. See Appendix 4 for specimen data.

of pale scales reflecting VHW band, noticeable only towards costal margin. VFW ground colour medium brown, slightly lighter in distal third; two or three tiny, barely noticeable yellow submarginal dots; rufous-brown, slightly undulate submarginal line. VHW medium brown, indistinct, "S"-shaped postdiscal line, a thin (≈ 1 mm) pale yellow postdiscal band from apex to tornus, nearly straight, passing along distal edge of discal cell at vein M3, in some individuals broken into a series of spots or completely absent; a thin, wavy submarginal darker brown line, area distal to it and immediately basal pale grey with a light magenta sheen. *Male genitalia*: as illustrated (Fig. 14B).

FEMALE (Fig. 8D): Similar to male except with a paler ventral surface.

Comments: Brown (1944) introduced the names *discontinua* and *neglecta* for two individual forms of "*M. lanassa*". The original illustrations of the holotype male genitalia of each, though poorly drawn, show the sparse, large dorsally directed spines at the tip of the valva, the very broad base of the valva, and the short, curved uncus and subunci that occur only in *M. ignilineata*. We have examined photographs of the holotypes of *neglecta* and *discontinua* (provided by Gerardo Lamas), now deposited in the AME, and both names apply to a population of *M. ignilineata* occurring in central Ecuador that appears to be consistently distinct from the nominate. Lamas & Viloria (2004) placed both names as synonyms of *M. ignilineata*, and since no other authors have dealt with Brown's names, we select *neglecta* as the name for this taxon (**n. stat.**). *Manerebia ignilineata*

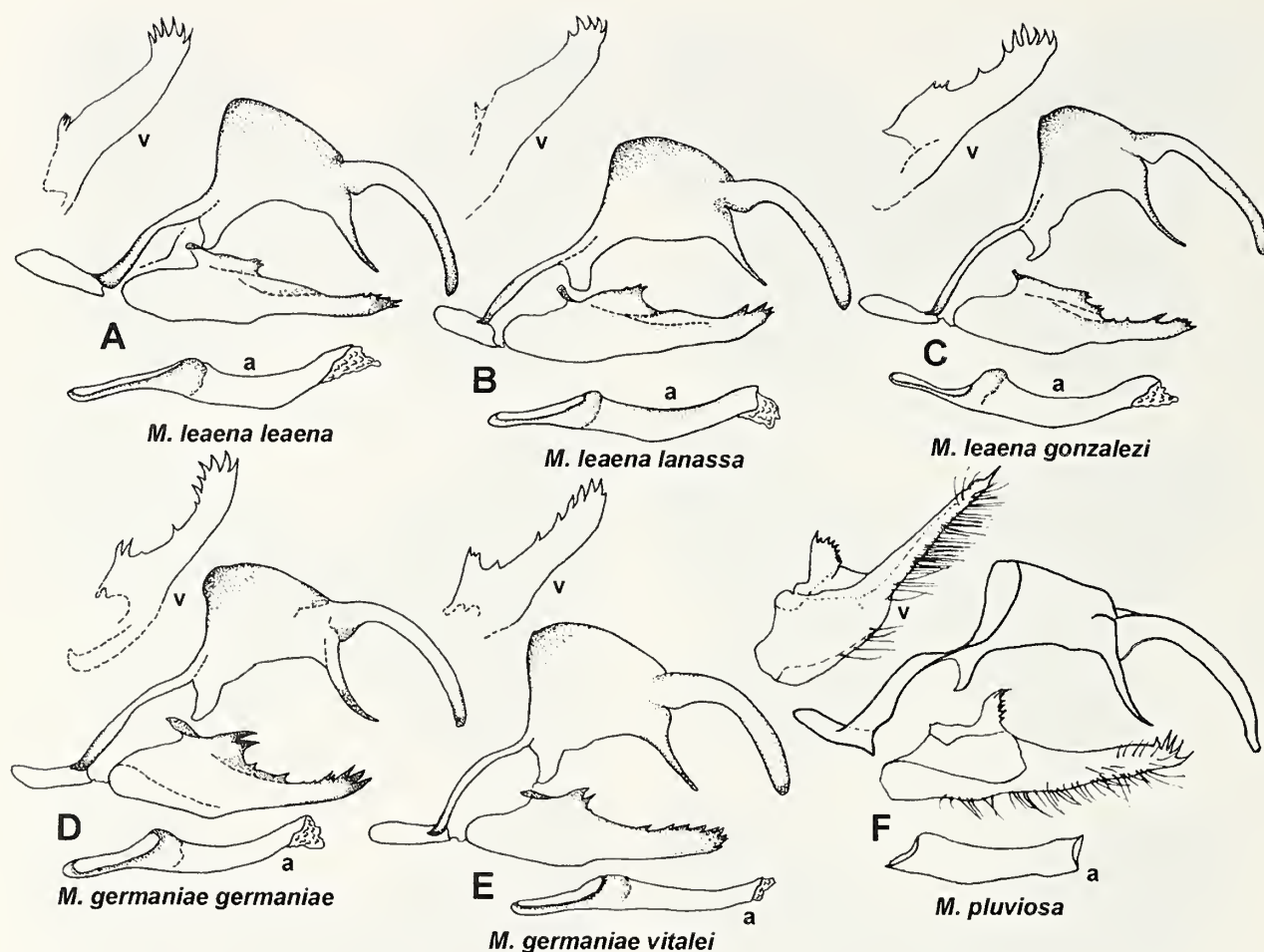


Fig. 10. *Manerebia* male genitalia, lateral view; v = valva ventral view, a = aedeagus lateral view, ad = aedeagus dorsal view. *M. leaena*, *M. germaniae* n. sp., *M. pluviosa* n. sp. See Appendix 5 for specimen data.

neglecta is known from Cañar: Pimo, Gun, Zhud-Alausí km 2, 3100 m; Tungurahua: Minza Chica, 3200 m; Napo: Papallacta-Archidona trail; Pichincha: Quito-Río Toachi trail; Chimborazo: Huigra; Hda. Licay, above Huigra; Bolívar: Pilaló, 3100 m south to Cañar, from 3100-3200 m. It is locally common in the forest-páramo ecotone near Zhud (Azuay), where it flies with *Neopetaliodes parrhoebia* n. ssp. and *Lymanopoda hazelana* n. ssp. (Pyrz, in prep.).

***Manerebia seducta* Pyrcz & Willmott, n. sp.**

Figs. 8E,F, 14C, 20

Manerebia n. sp. (Pyrz, Willmott & Hall); Lamas & Viloria (2004: 216, n. 1122).

Diagnosis: This species is recognised by the elongate shape of the wings, the white VHW band uniquely lying distal of the discocellulars, and by the small single ocelli on the fore and hindwing (absent in the female). The male genitalia are most similar to *M. ignilineata*, which may be the sister species, and are characterised by the broad base to the valva, with few terminal 'teeth', and elongate aedeagus. *Manerebia seducta* differs principally from *M. ignilineata* by the less reddish ground colour to the wings and more pointed forewing apex. The two species are microsympatric.

Description: MALE (Fig. 8E): **Head:** frons with a tuft of brown hair; labial palpi covered with dense and long black hair; eyes

blackish, smooth; antennae dorsally brown, ventrally chestnut, white scales at base of each segment. **Thorax:** dorsal and ventral surface dark brown; legs paler brown. **Abdomen:** dorsal and ventral surface dark brown. **Wings:** forewing (length: 23 mm, mean: 23 mm, n=2) elongate, triangular, with almost straight distal margin and sharply pointed apex; hindwing elongate and smoothly rounded, with no tornal notch. DFW uniform medium brown. DHW uniform medium brown. VFW ground colour medium brown, somewhat variable, slightly lighter towards outer margin; irregular dark brown submarginal line; area between it and outer margin suffused with magenta; a minute black ocellus with white pupil in cell Cu2-Cu1. VHW medium brown; barely visible, uneven, dark brown line through middle of discal cell, fading near costa and anal margin; thin, milky white postdiscal band from apex to tornus, with somewhat irregular inner and sharp outer edge; thin, smoothly curving darker brown submarginal line, parallel to distal margin, from tornus to near apex; thinner dark brown marginal line; the area between submarginal line and outer margin suffused with magenta, twice as wide as on the forewing. **Male genitalia:** (Fig. 14C) tegumen slender; uncus arched, subuncus half the length of uncus; valvae stout, sharply thinning at middle with three prominent distal 'teeth' and grooved dorsal surface; aedeagus long, thin and smooth, with a pronounced 'collar' at junction of anterior and

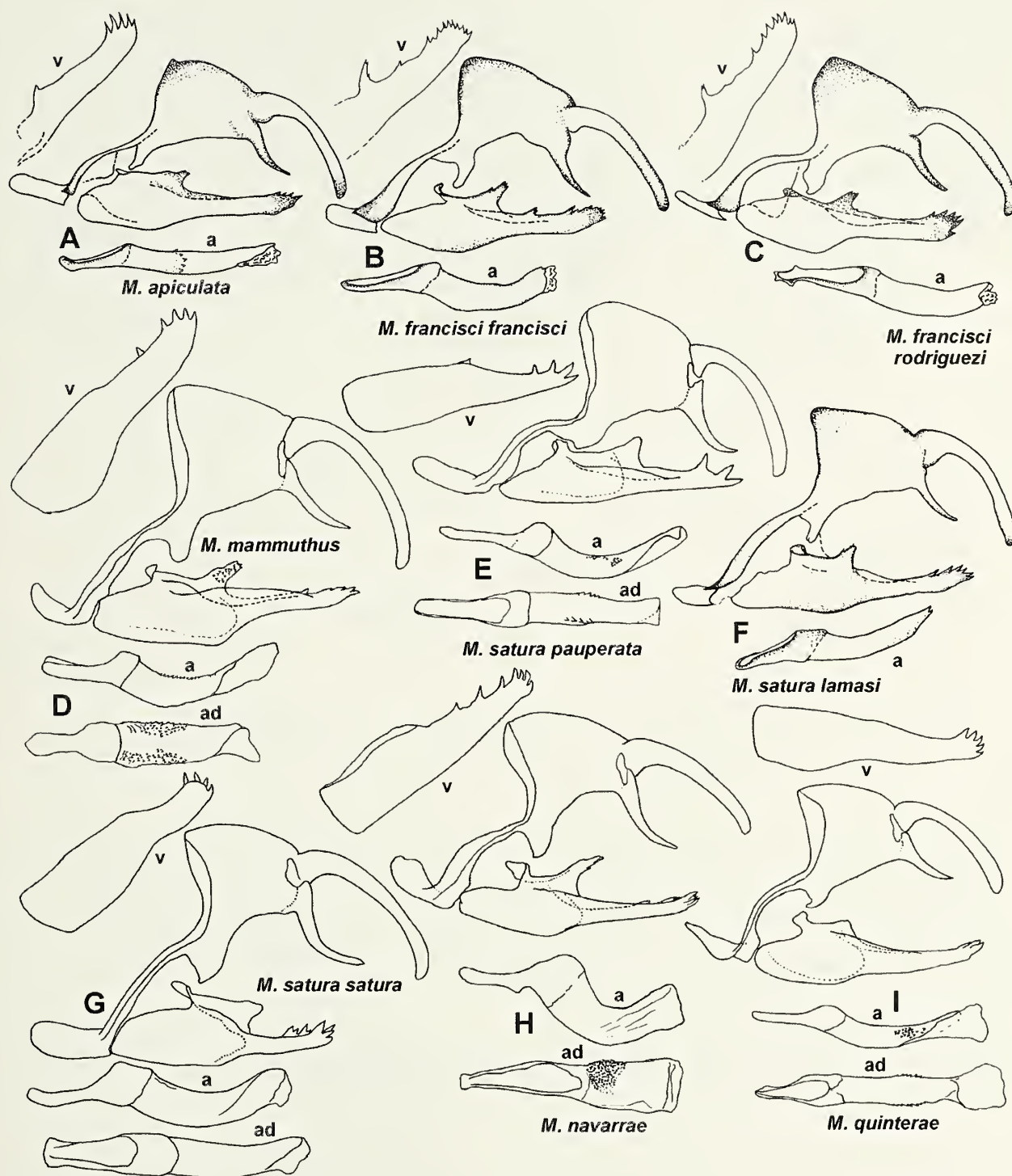


Fig. 11. *Manerebia* male genitalia, lateral view; v = valva ventral view, a = aedeagus lateral view, ad = aedeagus dorsal view. *M. apiculata*, *M. franciscae*, *M. mammothus* n. sp., *M. satura*, *M. navarrae*, *M. quinterae*. See Appendix 5 for specimen data.

posterior portions.

FEMALE: (Fig. 8F) *Head, thorax* and *abdomen* as in male. *Wings:* forewing (length: 17.5 mm, n=2) similar to male. DFW and DHW

uniform medium brown. VFW ground colour medium brown; basal two-thirds separated from distal third by sharp vertical boundary, basal two-thirds darker brown; minute paler submarginal dots in

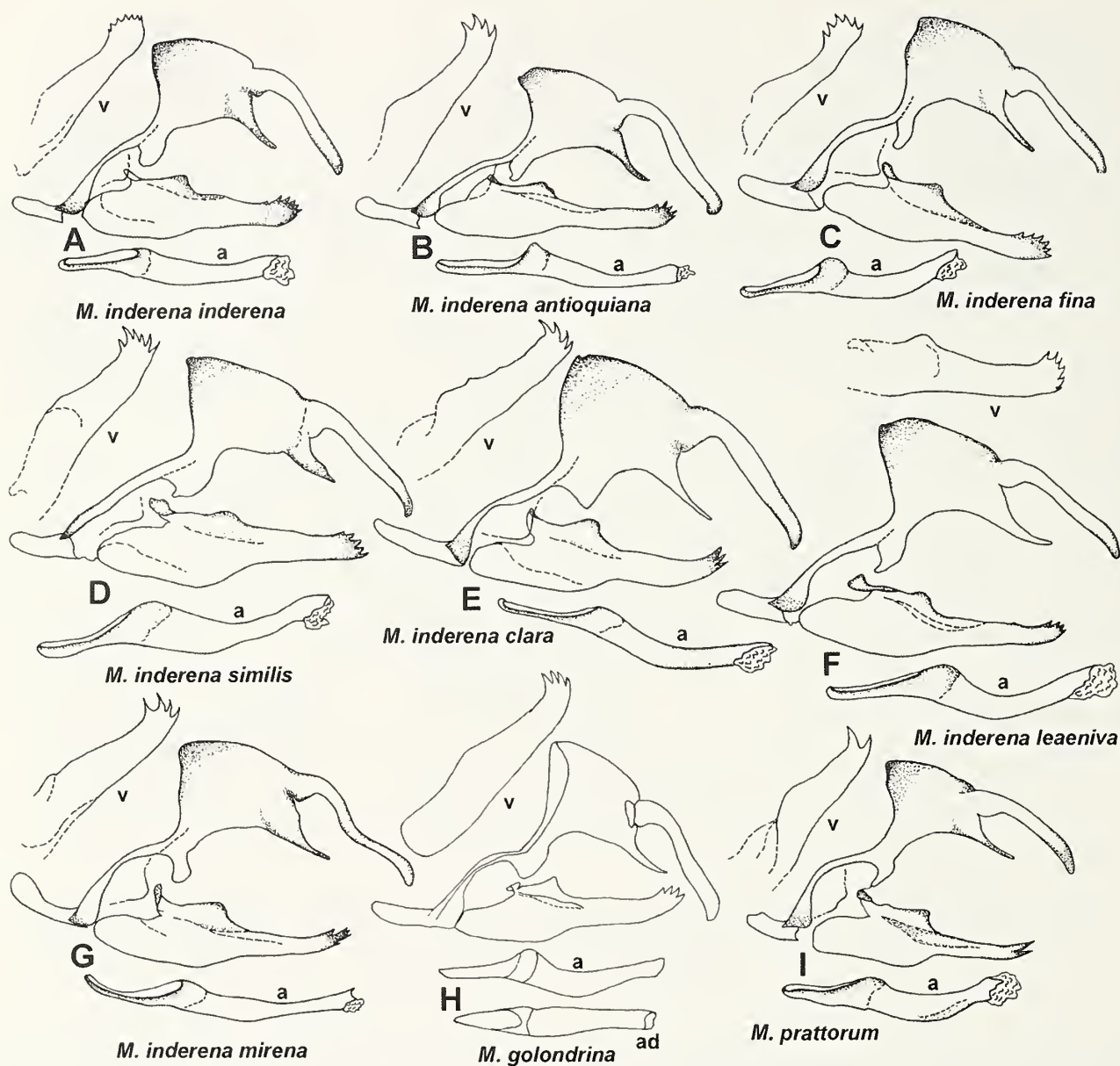


Fig. 12. *Manerebia* male genitalia, lateral view; v = valva ventral view, a = aedeagus lateral view, ad = aedeagus dorsal view. *M. inderena*, *M. golondrina* n. sp., *M. prattorum* n. sp. See Appendix 5 for specimen data.

centers of cells Cu2-Cu1 and Cu1-M3; thin distal marginal border of sparse, pale greyish scales. VHW medium brown; basal half with sparse, long brown hairs and scattered with very sparse paler brown scales; convex, uneven, dark brown line through middle of discal cell, fading near costa and anal margin; thin white postdiscal band from apex to tornus, broadest in cells Cu2-Cu1 to M3-M2, tapering to a point at costa and anal margin, lying distal of discocellulars; thin, smoothly curving darker brown submarginal line, parallel to distal margin, from tornus to near apex; marginal border distal of submarginal line dusted with sparse pale greyish scales.

Types: *Holotype* male: PERU, San Martín, Puerta del Monte, ca. 50 km NE Los Alisos, 3250 m, 22.VIII.1981, L.J. Barkley leg., MUSM;

Allotype female: ECUADOR: Loja, km 20 Jimbura-San Andrés rd., 3300 m, 24.IX.1997, K. Willmott leg., KWJH; *Paratype* male: PERU: San Martín, Parque Nacional Abiseo, Huicungo, Puerta del Monte, 3190-3250 m, 19.VII.1990, M. Medina leg., MUSM.

Etymology: The name of this species is the feminine form of the Latin adjective "seductus", meaning remote or distant, with reference to this species isolated range and rarity.

Comments: The two males of this species were collected in the Central Cordillera in northern central Peru, whereas the only known female specimen was collected in the Cordillera de Lagunillas in extreme southern Ecuador. *Manerebia seducta* thus has a wide, and as yet only roughly defined range. It is apparently a lower

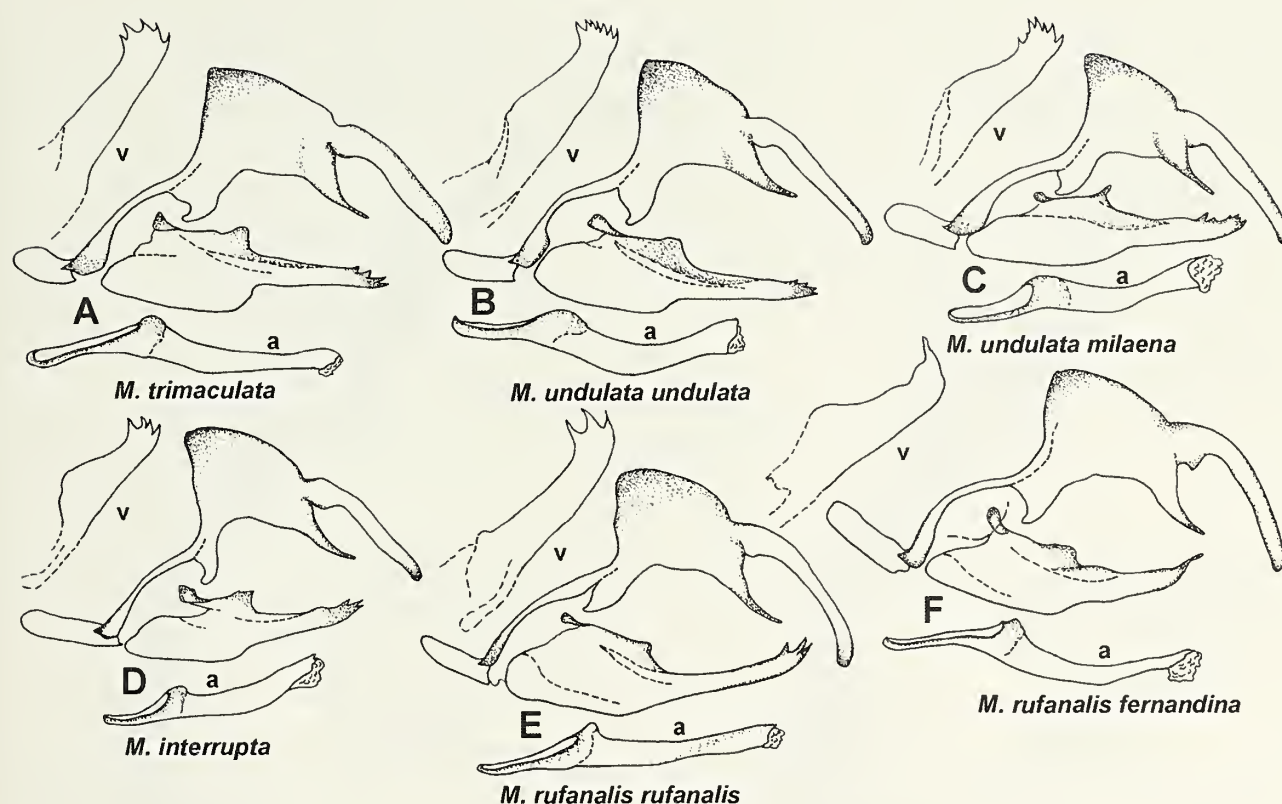


Fig. 13. *Manerebia* male genitalia, lateral view; v = valva ventral view, a = aedeagus lateral view, ad = aedeagus dorsal view. *M. trimaculata*, *M. undulata* n. sp., *M. interrupta*, *M. rufanalis* n. sp. See Appendix 5 for specimen data.

páramo grassland species, similar to *M. ignilineata*, which occurs sympatrically and much more abundantly in the same habitat. The elongate wings of the female of this species are similar to *M. levana*, and those of other páramo butterflies (e.g., the satyrine genus *Lymanopoda*, see Pyrcz *et al.*, 1999), and may be an adaptation to flying or resting in the strong winds that are frequent in these high elevation grasslands.

Manerebia mycalesoides (C. & R. Felder, 1867)

Figs. 8H, I, 14D, 20

Pronophila mycalesoides C. & R. Felder (1867: 473). **TL:** Colombia, Cundinamarca, Bogotá. **ST male:** BMNH(R) [examined] = *Euptychia lethe* Butler (1867: 465). **TL:** Venezuela. **ST males:** BMNH(R) [examined]

"*Penrosada*" *lethe* (Butler); D'Abbrera (1988: 824, fig.).

Pedaliodes mycalesoides (C. & R. Felder); Thieme (1905: 69).

Euptychia mycalesoides (C. & R. Felder); Weymer (1911: 224).

Posteuptychia mycalesoides Forster (1964: 137, fig. 171) (male genitalia).

Manerebia mycalesoides (C. & R. Felder); Lamas & Viloria (2004: 215).

Diagnosis: *Manerebia mycalesoides* is easily distinguished from all other congeners, except *M. magnifica*, by the large ventral ocelli on both fore and hindwing and wavy, dark, prominent postdiscal line on both VFW and VHW (Figs. 8H, I). The genitalia (Fig. 14D) are distinctive in the elongate distal part of the valva which is strongly curved upwards, ending with several short 'teeth', being most similar to *M. magnifica* and *M. nevadensis*. *Manerebia magnifica* is

distinguished under the account for that species.

Comments: *Pronophila mycalesoides* was described from Bogotá (Colombia) (C. & R. Felder, 1867), but the precise type locality is unknown and the species was not reported by Adams (1986). Shortly afterwards in the same year the same taxon was also described as *Euptychia lethe* by Butler (1867), from an unspecified Venezuelan locality. We have examined the syntypes of both names at the BMNH and *lethe* is a junior subjective synonym of *mycalesoides* (Lamas & Viloria, 2004). *Manerebia mycalesoides* seems to be a very rare species. It is found in lower cloud forest on the foothills of the Sierra de El Tamá at 1000 m. Nothing was known about the behavior or ecology of this species until Andrew Neild (pers. comm.) observed and collected it at Loma del Viento, Táchira, in 1997, where it flies in an open, windswept area, in association with bamboo. The range of the species has been extended by recent collecting, with records in the Venezuelan Cordillera de la Costa (San Antonio de Los Altos, Colonia Tovar), Sierra de El Tamá (San Vicente de La Revancha, Chorro El Indio), and the west Colombian Río Cauca valley (Popayán). *Manerebia mycalesoides* occurs in premontane rain forest habitats at around 1000 m, where it is a shy inhabitant of shady places within dense forest. Usually only single individuals are encountered, but Pierre Boyer (pers. comm.) observed on one occasion a large group of over ten males in a forest clearing in the Ávila range above Caracas.

Manerebia magnifica Pyrcz & Willmott, n. sp.

Figs. 8G, 14E, 20

Diagnosis: This species differs from its closest relative, *M.*

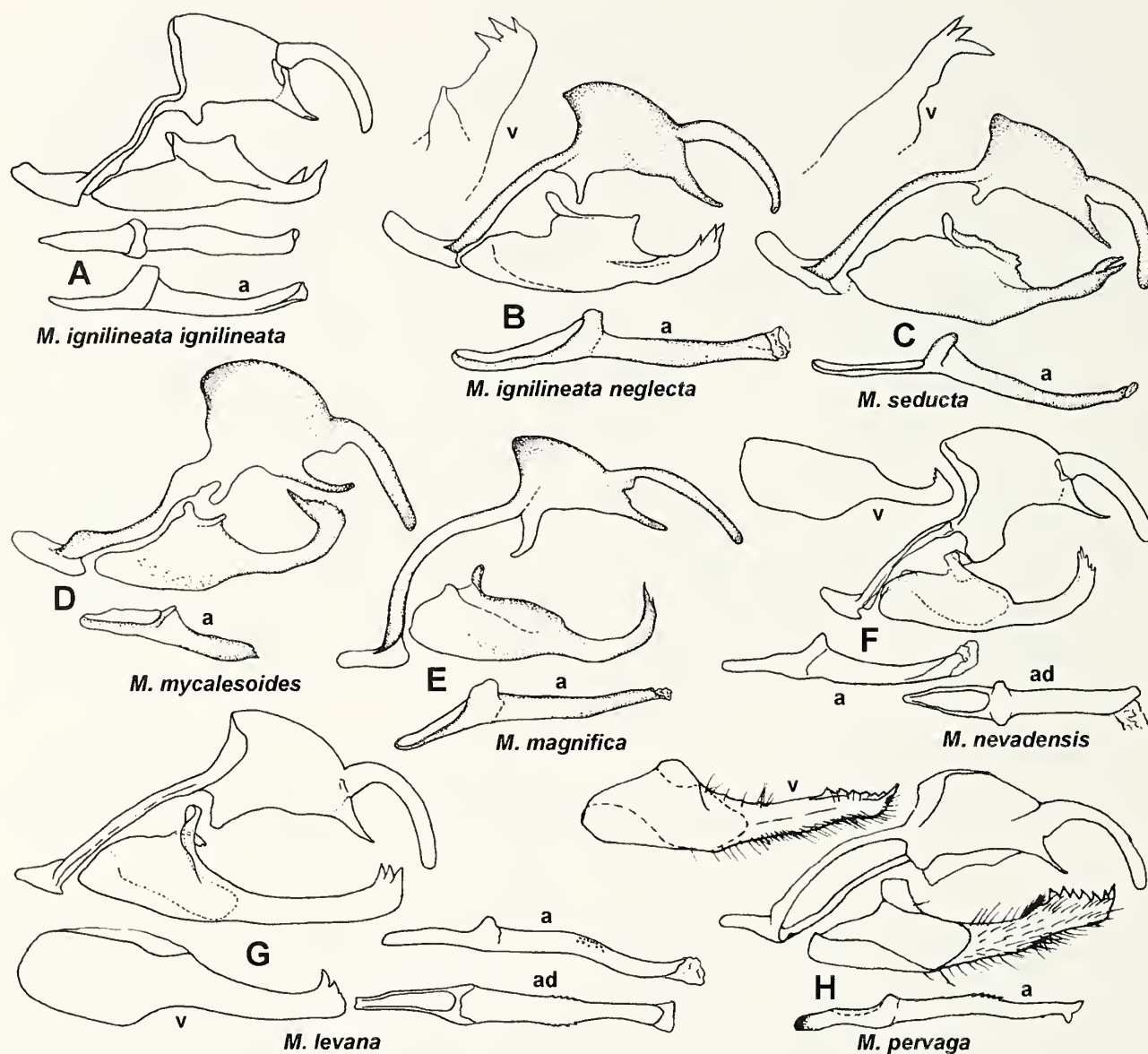


Fig. 14. *Manerebia* male genitalia, lateral view; v = valva ventral view, a = aedeagus lateral view, ad = aedeagus dorsal view. *M. ignilineata*, *M. seducta* n. sp., *M. mycalesoides*, *M. magnifica* n. sp., *M. nevadensis*, *M. levana*. See Appendix 5 for specimen data.

mycalesoides, in the larger size of the VHW submarginal ocelli, with an additional ocellus in cell Cu1-M3, and in their shape being oval instead of rounded. The distal tip of the valva is also less enlarged and recurved.

Description: MALE (Fig. 8G): **Head:** frons with a tuft of black hair; eyes black, smooth; labial palpi covered with long, black hair; antennae dorsally dark brown, ventrally chestnut, with white scales at the base of each segment, club same colour as shaft. **Thorax:** dorsal and ventral surface blackish brown; legs pale brown. **Abdomen:** dorsal surface blackish brown, ventrally grey. **Wings:** forewing (length: 23-24.5 mm, mean: 23.8 mm, n=3) distal margin straight, apex rounded; hindwing with distal margin very slightly angled at vein M3, tornal notch absent. DFW uniform dark brown; andro-

conial scales not apparent; faint blackish submarginal line. DHW dark brown, slightly paler towards distal margin, faint blackish submarginal line. VFW ground colour medium brown; indistinct, darker brown discal line running across discal cell, to base of vein Cu2, continuing towards anal margin; postdiscal line of same colour, bent distally in cell 1A-Cu2 to join submarginal line at tornus; submarginal line, and two dark brown thin marginal lines straight and parallel to outer margin; large (nearly width of cell), rounded, submarginal black ocellus with a white pupil and ringed with orange in cell Cu2-Cu1; another submarginal ocellus, half its size in cell M2-M1. VHW uniform medium brown; dark brown discal line from costa to inner margin, roughly parallel to outer margin, passing through base vein Cu2; dark brown postdiscal line,

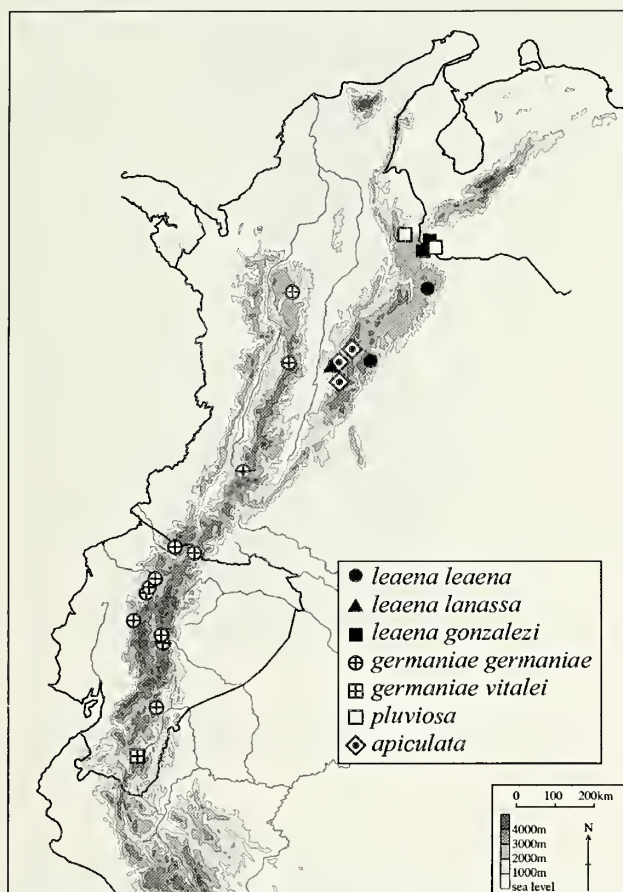


Fig. 15. Locality records for *Manerebia* in the northern Andes: *M. leaena*, *M. germaniae*, *M. pluviosa* and *M. apiculata*

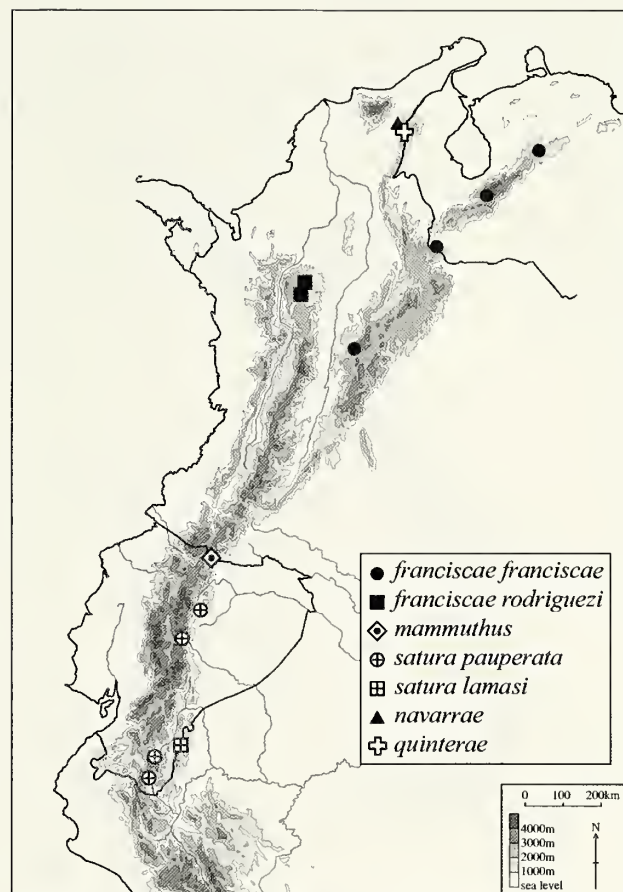


Fig. 16. Locality records for *Manerebia* in the northern Andes: *M. franciscae*, *M. mammuthus*, *M. satura*, *M. navarrae* and *M. quinterae*.

nearly straight, with the extremities curving slightly distally at apex and tornus to merge with a thinner submarginal dark brown line; submarginal line and two marginal lines parallel to outer margin; a series of black submarginal ocelli, four of them oval, two ocelli in cells 1A-Cu2, one each in Cu2-Cu1 and Cu1-M3, one rounded in cell M2-M1, the biggest of which is ocellus in Cu2-Cu1, extends to entire width of cell and nearly half of its length, remaining ocelli diminishing in size anteriorly and posteriorly, with tornal ocellus smallest; all ocelli ringed with orange, pupils in cells 1A-Cu2 and Cu2-Cu1 white, those in cells Cu1-M3 and M2-M1 blue; blue submarginal dot in cell M3-M2. **Male genitalia** (Fig. 14E): tegumen slender; uncus long and arched; subuncus rather short; extended apical part of the valva strongly curved upwards, ended with two 'teeth'; aedeagus straight with a pronounced 'collar' at junction of anterior and posterior portions

FEMALE: Unknown.

Types: *Holotype male*: PERU: Amazonas, Cordillera del Cóndor, alto Río Comaina, PV22, falso Paquisha, 800 m, 25.X.1987, G. Lamas *leg.*, MUSM; *Paratypes: 2 males*: same data as the holotype, MUSM.

Etymology: This species name is the feminine form of the Latin adjective, "magnificus", meaning magnificent, with reference to the impressive submarginal ocelli on the ventral surface.

Comments: This species is clearly most closely related to *M.*

mycalesoides, but the large apparent range disjunction between the two species and slight differences in the male genitalia suggest the two should be treated as distinct for the present. *Manerebia magnifica* is known so far only from the eastern slopes of the Cordillera del Cóndor in Peru, where it occurs in premontane forest. Its apparent absence in the heavily collected Zamora valley further west suggests it may be endemic to this isolated mountain range.

Manerebia nevadensis Krüger, 1925

Figs. 9A, B, 14F, 20

Manerebia nevadensis Krüger (1925: 25). **TL:** Colombia, Sierra Nevada de Santa Marta, 2600m. **LT male** (designated by Pycrz, 1999: 351): San Lorenzo, Sierra Nevada de Santa Marta, 06.IX.1919, 2600m, E. Krüger *leg.* MZPAN [examined].

Manerebia nevadensis Krüger, Adams & Bernard (1977: 273, fig. 17, male genit. fig. 5); Lamas & Viloria (2004: 215).

Diagnosis: *Manerebia nevadensis* superficially resembles some subspecies of *M. satura* in wing pattern, but the male genitalia (Fig. 14F) are strongly distinct from that species, instead indicating a relationship with *M. mycalesoides* and *M. magnifica*. All three of these species have a pronounced 'collar' at the junction of the anterior and posterior portion of the aedeagus, upturned tip to the valva and short subuncus, similar to certain southern Andean *Manerebia*

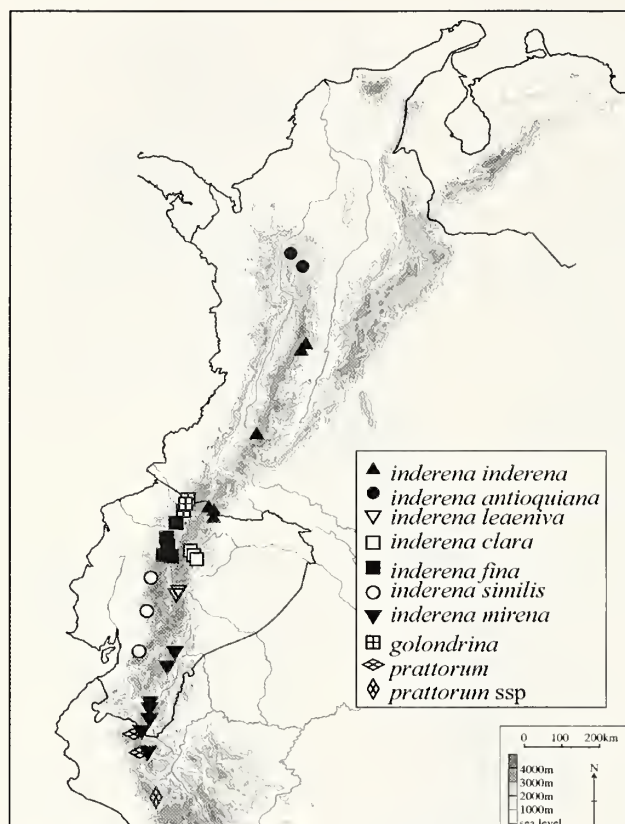


Fig. 17. Locality records for *Manerebia* in the northern Andes: *M. inderena*, *M. golondrina* and *M. prattorum*.

(e.g., *M. cyclopina* Staudinger).

Comments: This species is endemic to the Sierra Nevada de Santa Marta, where Adams & Bernard (1977) and Pyrcz (1999) report that it occurs from 2500–3000 m. It is an elusive butterfly, with a skipping flight, preferring to remain inside dense bamboo clumps and seldom coming to the edges.

Manerebia levana (Godman, 1905)

Figs. 9C, D, 14G, 20

Lymanopoda levana Godman (1905: 188, pl. 10, fig. 10). **TL:** Colombia, Cundinamarca, Bogotá. **ST male:** Colombia, Cundinamarca, Bogotá. BMNH [examined].

Penosada levana (Godman); Adams (1986: 307); Pyrcz (1999: 367).

Manerebia levana (Godman); Lamas & Vilorio (2004: 215).

Diagnosis: This is a small, very distinctive species, superficially resembling only *M. pervaga* and to some extent *M. navarrae*. The VHW postdiscal band is yellowish, indistinct, oblique and marked at its distal edge by a thin, dentate and dark brown line, dividing the wing into an yellow-orange area basally and a chestnut area distally. The ventral submarginal ocelli are much reduced, with only a small one in cells 1A–Cu2 on the VHW and VFW. Further distinguishing characters are discussed under *M. pervaga*. The male genitalia resemble only those of *M. pervaga*. These two species are unique within *Manerebia* in having a highly elongate distal portion of the valva and elongate aedeagus, bearing two dorso-lateral patches of spines in the middle of the posterior section. The relationships of

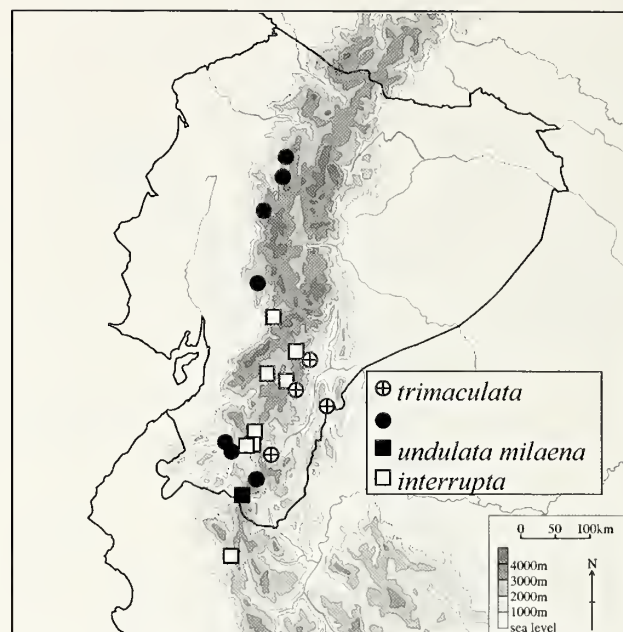


Fig. 18. Locality records for *Manerebia* in the northern Andes: *M. trimaculata*, *M. undulata* and *M. interrupta*

the species to other congeners are uncertain. *M. levana* is geographically variable and it remains possible that distinct subspecies will be recognised in future. Male genitalia as illustrated (Fig. 14G).

Comments: Although Adams (1986) reports this species from Panama, based on specimens in the BMNH, these are definitely mislabelled. The species is known from both slopes of the Colombian Cordillera Oriental in the Bogotá region (Cerro Monserrate) from 2700–3300 m, and Adams (1986) found it in páramo grassland between bamboo-filled gullies at the tree-line. Krüger (1924) described the female of this species (Pyrcz, 1999).

Manerebia pervaga Pyrcz & Vilorio, n. sp.

Figs. 9E, F, 14H, 20

Manerebia n. sp. (Pyrcz & Vilorio); Lamas & Vilorio (2004: 216, n. 1121).

Diagnosis: This species differs from *M. levana* in several characters. The VHW is more uniformly coloured in the male, while the female is uniformly brown, lacking the yellowish colouring of *M. levana*. Both sexes lack tornal ocelli on both wings and the dark postdiscal line on the VHW is more basally positioned, being present in cell 2A–Cu2 (absent in *M. levana*). The female has a strongly dentate thin brown marginal line that is more basally positioned, and the forewing, and to a lesser extent the hindwing, are much more rounded than in *M. levana*. Finally, both sexes have a dark discocellular streak between the bases of veins M2 and M1 on the hindwing (also on the forewing in the female) that is unique in the genus.

Description: MALE (Fig. 9E): **Head:** frons with a tuft of dark brown hair; eyes dark coffee brown, smooth; labial palpi slightly longer than head, with light brown and black hairs; antennae with club twice as broad as shaft, orange brown, darker dorsally. **Thorax:** moderately hairy, more densely on ventral surface, dorsally blackish brown, ventrally brown; legs medium brown. **Abdomen:** dark brown, lighter on ventral surface, especially at posterior tip. **Wings:** forewing (length: 16.5–17.5; mean: 17 mm; n=3) triangular, tornus

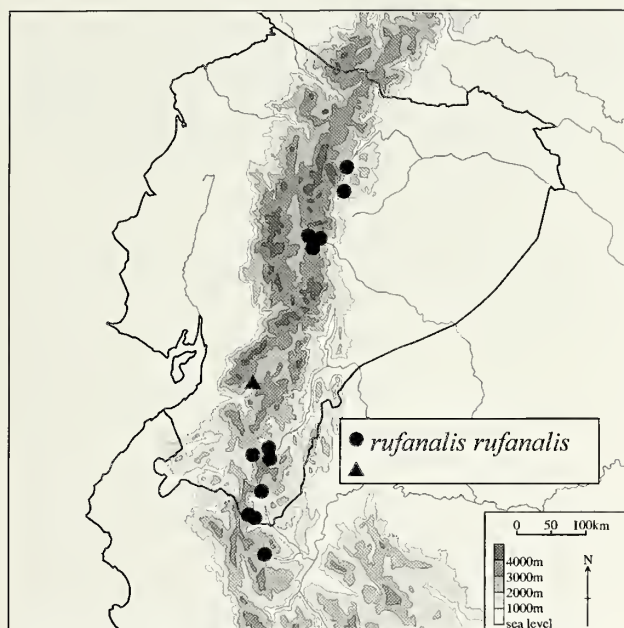


Fig. 19. Locality records for *Manerebia* in the northern Andes: *M. rufanalis*

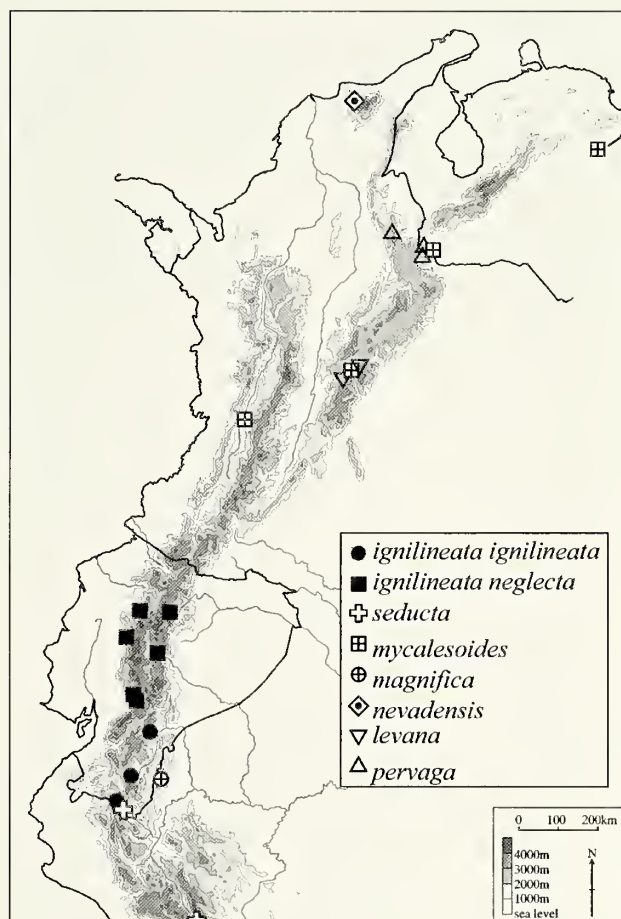


Fig. 20. Locality records for *Manerebia* in the northern Andes: *M. ignilineata*, *M. seducta*, *M. mycalesoides*, *M. magnifica*, *M. nevadensis*, *M. levana* and *M. pervaga*.

obtuse; hindwing rounded, tornus moderately pointed, anal margin straight; dorsal surface of both wings hairy in basal half and along anal margin. Dorsal surface ground colour coffee brown; diffuse orange patch on DHW tornus. VFW ground colour chocolate brown, slightly darkened at base; costal margin lighter; distal margin, apical, and subapical region ochraceous brown (with reddish tone towards anterior edges), as well as base of costal margin region. VHW ground colour yellowish brown, darker at basal region; light suffusion of orange towards posterior postdiscal region, forming diffuse irregular wedge bordered distally with thin dark brown dentate postdiscal line, fading anteriorly and posteriorly and parallel to distal margin, in cells 2A-Cu2 to M2-M1. **Male genitalia** (Fig. 14H): similar to *M. levana* with elongate distal tip to valva, except dorsal 'teeth' at distal tip of valva more extensive, extending anteriorly; aedeagus similar to *M. levana*, elongate, with two dorso-lateral patches of spines in middle of posterior section.

FEMALE (Fig. 9F): **Head**: frons with a tuft of brown hair; eyes medium brown, smooth; labial palpi 2.5 times length of head, with long brown hair; antennae with club three times as thick as basal segments, shaft dorsally and ventrally light brown, club ventrally orange, dorsally blackish brown. **Thorax**: moderately hairy, more densely on ventral surface, dorsally blackish brown, ventrally brown; legs medium brown. **Abdomen**: dorsally blackish brown, laterally and ventrally medium brown. **Wings**: forewing (length: 16.5-17.5 mm; mean: 17 mm; n=2) costa slightly arched, apex blunt, distal margin and tornus rounded. Hindwing overall triangular, with apex, tornus and margins smoothly rounded. Dorsal surface uniform medium brown; fringes light grey. VFW greyish brown, darker brown in basal half; darker brown streak over discocellulars between bases of veins M1 and M2. VHW greyish brown, darker brown at base and posterior of discal cell; darker brown streak over discocellulars between bases of veins M1 and M2; postdiscal dark brown line composed of lunular streaks incurved basally in cells M2-M1 to 1A-Cu2, approximately parallel to distal margin; faint dark brown

submarginal 'V'-shaped streaks in cells M1-Rs to 1A-Cu2.

Material examined: **Holotype male**: VENEZUELA: Táchira, Parque Nacional El Tamá, Venezuela, 3100-3350 m, 16-18.II.1992, A. Viloria & J. Camacho leg., MALUZ; **Allotype female**: COLOMBIA: Norte de Santander, Cerro Oroque, 3850 m, 12.VI.1965, J. Bechyné leg., MIZA; **Paratypes (3 males)**: VENEZUELA: **1 male**: same data as the holotype, MALUZ; **1 male**: Páramo El Tamá, 2600m, 12.II.1983, M. Vivas leg., MIZA; COLOMBIA: **1 male**: Norte de Santander, Páramo El Tamá vía Herrán, XII.1993, J. F. Le Crom leg., JFLC; **1 female**: same data as allotype, MIZA.

Etymology: The name is the feminine form of the Latin adjective "pervagus", meaning wandering, in reference to the flight of this species in the páramo grassland.

Comments: *Manerebia pervaga* is known from the Sierra de El Tamá on the Venezuela/Colombia border and the Cerro Oroque in Norte de Santander in Colombia. It occurs in open páramo covered with low growing *Chusquea* thickets from 3200-3850 m. This is higher than that reported for any other congeners, even páramo species like *M. seducta*, *M. ignilineata* and *M. levana*. *Manerebia pervaga* shares with the last two of these species its small size and dull, cryptic colours, which may be adaptations to páramo habitats and not necessarily indicate any close affinity. This species seems to be seasonal and has only been found flying during the dry season, on days with bright, direct sunlight.

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APPENDIX 1. Errors in main references on north Andean *Manerebia*

Brown (1944):

Penrosada leaena = *Manerebia inderena leaeniva*

Penrosada apiculata = *Manerebia interrupta*

Penrosada lanassa = *Manerebia ignilineata*

D'Abrera (1988):

Penrosada leaena (dorsal surface) = *Manerebia undulata*

Penrosada leaena (ventral surface) = *Manerebia* n. sp., Peru (Pyrz, in prep.)

Penrosada lanassa (dorsal surface) = *Manerebia rufanalis rufanalis*

Penrosada lanassa (ventral surface) = *Manerebia satura satura*

Penrosada sp. = *Manerebia satura pauperata*

Euptychia jovita = *Manerebia satura pauperata*

Penrosada lethe = *Manerebia mycalesoides*

Adams (1986):

Penrosada inderena male holotype = *Penrosada inderena* female paratype

APPENDIX 2. Distribution of taxa along hypothetical elevational transects

Approximate elevational range	Ecuador, Zamora-Chinchi, E. slope	Ecuador, Pastaza, E. slope	Colombia, Choachí, E. cordillera, E slope	Colombia, El Tamá E. cordillera, NE tip
1000-1400m	<i>magnifica</i>	-	<i>mycalesoides</i>	<i>mycalesoides</i>
1400-1800m	<i>satura pauperata</i>	<i>satura pauperata</i>	<i>francisciae francisciae</i>	<i>francisciae francisciae</i>
1800-2200m	<i>rufanalis rufanalis</i>	<i>rufanalis rufanalis</i>	-	-
2200-2600m	<i>trimaculata</i>	-	-	-
2600-3000m	<i>inderena mirena</i>	<i>inderena leaeniva</i>	<i>leaena leaena</i>	<i>leaena gonzalezi</i>
2800-3200m	<i>germaniae vitali</i>	<i>germaniae germaniae</i>	<i>apiculata</i>	<i>pluviosa</i>
3000-3400m	<i>ignilineata ignilineata</i>	<i>ignilineata neglecta</i>	<i>levana</i>	<i>pervaga</i>
3200-3600m	<i>seducta</i>	-	-	<i>pervaga</i>
Total species	8	5	5	5

APPENDIX 3. Distribution of taxa by country

Species	Subspecies	Ecuador	Colombia	Venezuela	North Peru
<i>leaena</i>	<i>leaena</i>	-	+	-	-
	<i>lanassa</i>	-	+	-	-
	<i>gonzalezi</i>	-	+	+	-
<i>germaniae</i>	<i>germaniae</i>	+	+	-	+
	<i>vitali</i>	+	-	-	-
<i>pluviosa</i>		-	+	+	-
<i>apiculata</i>		-	+	-	-
<i>navarrae</i>		-	+	+	-
<i>golondrina</i>		+	+	-	-
<i>satura</i>	<i>pauperata</i>	+	-	-	-
	<i>lamasi</i>	+	-	-	+

APPENDIX 3 (Cont)

Species	Subspecies	Ecuador	Colombia	Venezuela	North Peru
<i>mammuthus</i>		+	+	-	-
<i>franciscæ</i>	<i>franciscæ</i>	-	+	+	-
	<i>rodriguezi</i>	-	+	-	-
<i>ignilineata</i>	<i>ignilineata</i>	+	-	-	+
	<i>neglecta</i>	+	-	-	-
<i>inderena</i>	<i>inderena</i>	-	+	-	-
	<i>antioquiiana</i>	-	+	-	-
	<i>laeniva</i>	+	-	-	-
	<i>clara</i>	+	-	-	-
	<i>similis</i>	+	-	-	-
	<i>finæ</i>	+	+	-	-
	<i>mirena</i>	+	-	-	+
<i>prattorum</i>		-	-	-	+
<i>trimaculata</i>		+	-	-	+
<i>undulata</i>	<i>undulata</i>	+	-	-	-
	<i>milaena</i>	+	-	-	+
<i>interrupta</i>		+	-	-	+
<i>rufanalis</i>	<i>rufanalis</i>	+	-	-	+
	<i>fernandina</i>	+	-	-	-
<i>quinteræ</i>		-	+	+	-
<i>nevadensis</i>		-	+	-	-
<i>levana</i>		-	+	-	-
<i>pervaga</i>		-	+	+	-
<i>mycalesoides</i>		-	+	+	-
<i>magnifica</i>		+	-	-	+
<i>seducta</i>		+	-	-	+
TOTAL 23	37	sp12/ssp22	sp14/ssp20	sp7/ssp7	sp11/ssp11

APPENDIX 4. Figured specimens

Species	Subspecies	Locality	Sex	Type	Coll.	Fig.
<i>laena</i>	<i>laena</i>	Colombia, Cundinamarca: Guasca-Gachetá	M		BMNH (A&B)	1A
	<i>laena</i>	Colombia, Cundinamarca: "Bogotá"	F		TWP	1B
	<i>lanassa</i>	Colombia, Boyacá: W below Arcabuco	M		BMNH(A&B)	1C
	<i>lanassa</i>	Colombia, Boyacá: W below Arcabuco	F		BMNH(A&B)	1D
	<i>gonzalezi</i>	Venezuela, Táchira: Sierra de El Tamá	M	PT	TWP	1E
<i>germaniae</i>	<i>germaniae</i>	Ecuador, Cotopaxi: Pilaló	M	HT	MZUJ	1F
	<i>germaniae</i>	Ecuador, Cotopaxi: Pilaló	F	AT	TWP	1G
	<i>vitalei</i>	Ecuador, Zamora: Loja-Zamora old rd.	M	HT	MZUJ	1H
<i>pluviosa</i>		Venezuela, Táchira: San Vicente de la Revancha	M	PT	TWP	2A
<i>apiculata</i>		Colombia, Cundinamarca: "Bogotá"	M		BMNH	2B
<i>apiculata</i>		Colombia, Cundinamarca: "Bogotá"	F		MIZPAN	2C
<i>franciscæ</i>	<i>franciscæ</i>	Venezuela, Mérida: above La Montaña	M	PT	BMNH(A&B)	2D
	<i>franciscæ</i>	Venezuela, Mérida: above La Montaña	F	PT	BMNH(A&B)	2E
	<i>rodriguezi</i>	Colombia, Antioquia: Guarné	M	HT	MZUJ	2F
	<i>rodriguezi</i>	Colombia, Antioquia: El Retiro	F	AT	TWP	2G
<i>mammuthus</i>		Ecuador, Sucumbíos: El Higuerón	M	HT	AME	2H
<i>satura</i>	<i>satura</i>	Peru, Puno: Carabaya, Santo Domingo	M		BMNH(R)	3A
	<i>lamasi</i>	Peru, Amazonas: Alfonso Ugarte	M	HT	MUSM	3B
	<i>pauperata</i>	Ecuador, Zamora: Loja-Zamora rd. km 40	M	HT	MZUJ	3C
	<i>pauperata</i>	Ecuador, Zamora: Loja-Zamora rd. km 40	F	AT	TWP	3D
<i>navarrae</i>		Colombia, César: S. de Valledupar, Finca Altamira	M	PT	BMNH(A&B)	3E
<i>quinteræ</i>		Venezuela, Zulia: E. above Manaure	M	PT	BMNH(A&B)	3F
<i>inderena</i>	<i>inderena</i>	Colombia, Tolima: S above Cajamarca	M	HT	BMNH(A&B)	3G
	<i>inderena</i>	Colombia, Tolima: S above Cajamarca	F	PT	BMNH(A&B)	3H
	<i>antioquiiana</i>	Colombia, Antioquia: El Retiro	M	HT	MZUJ	4A
	<i>antioquiiana</i>	Colombia, Antioquia: El Retiro	F	AT	TWP	4B

APPENDIX 4 (Cont)

Species	Subspecies	Locality	Sex	Type	Coll.	Fig.
	<i>finia</i>	Ecuador, Pichincha: Aloag-Santo Domingo rd.	M	PT	KWJH	4C
	<i>finia</i>	Ecuador, Pichincha: Volcán Paschoa	F	PT	KWJH	4D
	<i>similis</i>	Ecuador, Bolívar: Balzapamba, arriba de Sta. Lucía	M	HT	MZUJ	4E
	<i>similis</i>	Ecuador, Azuay: Molleturo	F	PT	TWP	4F
	<i>clara</i>	Ecuador, Napo: Baeza	M	PT	TWP	4G
	<i>clara</i>	Ecuador, Napo: Hda. San Isidro	F	AT	PB	4H
	<i>miarena</i>	Ecuador, Loja: Cajanuma	M	PT	TWP	5A
	<i>miarena</i>	Ecuador, Loja: km 95-100 Loja-Zumba rd.	F	AT	PB	5B
	<i>leavenia</i>	Ecuador, Tungurahua: El Tablón	M	PT	TWP	5C
<i>golondrina</i>		Ecuador, Carchi: Santa Rosa, Las Golondrinas	M	PT	KWJH	5D
<i>prattorum</i>		Peru: "West slopes of Andes"	M	PT	BMNH(R)	5E
<i>trimaculata</i>		Ecuador, Zamora-Chinchipe: Río San Francisco	M		TWP	5F
<i>trimaculata</i>		Ecuador, Zamora-Chinchipe: Loja-Zamora rd.	M		TWP	5G
<i>trimaculata</i>		Ecuador, Morona-Santiago: km 37 Limón-Gualaceo	F		KWJH	5H
<i>undulata</i>	<i>undulata</i>	Ecuador, Pichincha: Tandapi	M	PT	KWJH	6A
	<i>undulata</i> ?	Ecuador, Loja: Yangana, Valladolid rd.	M		TWP	6B
	<i>undulata</i>	Ecuador, Bolívar: Balzapamba, arriba de Sta. Lucía	F	AT	TWP	6C
	<i>milana</i>	Ecuador, Loja: Jimbura-Laguna Negra rd.	M	HT	MZUJ	6D
<i>interrupta</i>		Ecuador, Azuay: Sigüig-Granadillas	M		TWP	6E
<i>interrupta</i>		Ecuador, Azuay: Sigüig-Granadillas	M		TWP	6F
<i>interrupta</i>		Ecuador, Azuay: Sigüig-Granadillas	M		TWP	6G
<i>interrupta</i>		Ecuador, Azuay: Sayausí	F		TWP	6H
<i>rufanalis</i>	<i>rufanalis</i>	Ecuador, Tungurahua: Runtún	M	HT	MZUJ	7A
	<i>rufanalis</i>	Ecuador, Zamora-Chinchipe: Loja-Zamora old rd.	F	AT	MBLI	7B
	<i>fernandina</i>	Ecuador, Girón: San Fernando	M	HT	MZUJ	7C
<i>ignilineata</i>	<i>ignilineata</i>	Ecuador, Morona-Santiago: Gualaceo-Limón rd.	M		TWP	7D
	<i>ignilineata</i>	Ecuador, Loja: Loja	M		TWP	7E
	<i>ignilineata</i>	Ecuador, Loja: Loja-Zamora rd.	M		TWP	7F
	<i>ignilineata</i>	Ecuador, Morona-Santiago: Gualaceo-Limón rd.	F		TWP	7G
	<i>neglecta</i>	Ecuador, Bolívar: Pilaló	M		TWP	8A
	<i>neglecta</i>	Ecuador, Cañar: Zhud	M		TWP	8B
	<i>neglecta</i>	Ecuador, Bolívar: Pilaló	M		TWP	8C
	<i>neglecta</i>	Ecuador, Cañar: Zhud	F		TWP	8D
<i>seducta</i>		Peru, San Martín: Puerta del Monte	M	HT	MUSM	8E
<i>seducta</i>		Ecuador, Loja: Jimbura-San Andrés rd.	F	AT	KWJH	8F
<i>magnifica</i>		Peru, Amazonas: Falso Paquisha	M	HT	MUSM	8G
<i>mycalesoides</i>		Venezuela, Miranda: Altos de Pipe	M		AFEN	8H
<i>mycalesoides</i>		Venezuela, Táchira: Loma del Viento	F		AFEN	8I
<i>nevadensis</i>		Colombia: S. Nevada de Santa Marta, El Campano	M		BMNH(A&B)	9A
<i>nevadensis</i>		Colombia: Sierra Nevada de Santa Marta	F	PLT	MIZPAN	9B
<i>levana</i>		Colombia: "Interior of Colombia"	M		BMNH	9C
<i>levana</i>		Colombia, Tolima: Río Chili	F		BMNH	9D
<i>pervaga</i>		Venezuela, Táchira: Sierra de El Tamá	M	HT	MALUZ	9E
<i>pervaga</i>		Colombia, Norte de Santander: Cerro Oroque	F	PT	MIZA	9F

APPENDIX 5. Male genitalic dissections

Species	Subspecies	Locality	Type	Coll.	Dissection#	Fig.
<i>leana</i>	<i>leana</i>	Colombia, Cundinamarca: "Env. Bogotá"		BMNH	6443	
	<i>leana</i>	Colombia, Cundinamarca: Choachi		TWP	02/02.05.1999	10A
	<i>leana</i>	Colombia, Cundinamarca: Choachi		BMNH	6441	
	<i>leana</i>	Colombia, Cundinamarca: Guasca-Gachetá		BMNH	6442	
	<i>leana</i>	Colombia, Boyacá: Sierra Nevada del Cocuy		BMNH		
	<i>leana</i>	No data: "¿Ecuador/Quito"	LT	BMNH		
	<i>lanassa</i>	Colombia, Cundinamarca: Facatativa		TWP	04/07.04.1999	10B
	<i>lanassa</i>	Colombia: Santander		TWP		
	<i>lanassa</i>	Colombia, Cundinamarca: "Bogotá"	HT	BMNH	29877	
	<i>gonzalezi</i>	Venezuela, Táchira: Sierra de El Tamá	PT	TWP	05/07.04.1999	10C

APPENDIX 5 (Cont.)

Species	Subspecies	Locality	Type	Coll.	Dissection#	Fig.
<i>germaniae</i>	<i>germaniae</i>	Colombia, Cauca: Puracé	PT	TWP		
	<i>germaniae</i>	Ecuador, Pichincha: Quito-Sto. Domingo old rd.	PT	KWJH	PENROS 12	
	<i>germaniae</i>	Ecuador, Pichincha: Yanacocha	PT	KWJH		
	<i>germaniae</i>	Ecuador, Pichincha: above Chiriboga	PT	BMNH	6451	
	<i>germaniae</i>	Ecuador, Cotopaxi: Pilaló	PT	TWP	01/26.01.1999	10D
	<i>germaniae</i>	Ecuador, Tungurahua: El Tablón	PT	MBLI		
<i>pluviosa</i>	<i>vitalei</i>	Ecuador, Zamora-Chinchipe: Loja-Zamora rd.	PT	MBLI	2003-12-23	10E
		Venezuela, Táchira: Sierra de El Tamá	PT	TWP		10F
<i>apiculata</i>		Colombia, Cundinamarca: Zipaquirá		TWP	05/30.03.1999	11A
<i>franciscæ</i>	<i>franciscæ</i>	Venezuela, Mérida: Mérida	PT	BMNH	6436	
	<i>franciscæ</i>	Venezuela, Táchira: Sierra de El Tamá		TWP	01/02.05.1999	11B
	<i>franciscæ</i>	Colombia, Cundinamarca: Pacho		TWP		
	<i>rodriguezi</i>	Colombia, Antioquia: El Retiro	PT	TWP	01/21/12/2003	11C
<i>mammuthus</i>		Ecuador, Sucumbíos: El Higuérón	HT	KWJH	PENROS 8	11D
<i>mammuthus</i>		Ecuador, Sucumbíos: El Higuérón	PT	KWJH	MAN 1	
<i>satura</i>	<i>pauperata</i>	Ecuador, Napo: Sierra de los Huacamayos	PT	TWP	02/31.03.1999	11E
	<i>pauperata</i>	Ecuador, Pastaza: "Env. d'Ambato"	PT	BMNH	6455	
	<i>pauperata</i>	Ecuador, Zamora-Chinchipe: Loja-Zamora rd.	PT	KWJH	PENROS 9	
	<i>lamasi</i>	Peru, Amazonas: Alfonso Ugarte	PT	MUSM	06/27.04.2002	11F
	ssp	Peru, Cajamarca: La Balsa		MUSM		
	<i>satura</i>	Peru, Puno: Santo Domingo		BMNH	6454	11G
	<i>satura</i>	No data: "Cauca valley, Colombia" - error		BMNH	6437	
		Colombia, César: Sierra de Perijá	PT	BMNH	29913	11H
		Colombia, César: Sierra de Perijá	PT	MA		
		Venezuela, Zulia: E. above Manaure	PT	BMNH	6445	11I
<i>navarrae</i>	<i>quinterae</i>	Colombia, Caldas: Páramo de Letras		TWP		
	<i>quinterae</i>	Colombia, Tolima: S. above Cajamarca		BMNH	6453	
	<i>quinterae</i>	Colombia, Rurillo		TWP	09/30.03.1999	12A
	<i>quinterae</i>	Ecuador, Sucumbíos: Qbda. de Piedras		KWJH	PENROS 13	
	<i>quinterae</i>	Ecuador, Sucumbíos: El Higuérón		KWJH	PENROS 19	
	<i>quinterae</i>	Colombia, Antioquia: El Retiro	PT	TWP	05/11.12.2003	12B
	<i>quinterae</i>	Ecuador, Pichincha: Nono-Nanegalito rd.	PT	TWP	03/31.03.1999	12C
	<i>quinterae</i>	Ecuador, Pichincha: Qbda. Molino	PT	KWJH	PENROS 3	
	<i>quinterae</i>	Ecuador, Pichincha: Aloag-Sto. Domingo rd.	PT	KWJH	PENROS 6	
	<i>quinterae</i>	Ecuador, Pichincha: Aloag-Sto. Domingo rd.	PT	KWJH	PENROS 4	
	<i>quinterae</i>	Ecuador, Pichincha: Volcán Pasochoa	PT	TWP		
	<i>quinterae</i>	Ecuador		BMNH	6439	
	<i>quinterae</i>	Ecuador, Bolívar: Balzapamba	PT	TWP	04/25.01.1999	12D
	<i>quinterae</i>	Ecuador, Napo: Río Chonta	PT	KWJH		
	<i>quinterae</i>	Ecuador, Napo: Baeza	PT	TWP	06/25.01.1999	12E
	<i>quinterae</i>	Ecuador, Tungurahua: Volcán Tungurahua	PT	TWP	08/07.04.1999	12F
	<i>quinterae</i>	Ecuador, Tungurahua: Río Verde Chico	PT	TWP		
	<i>quinterae</i>	Ecuador, Tungurahua: Baños	PT	BMNH	6457	
	<i>quinterae</i>	Ecuador	PT	BMNH	6456	
	<i>quinterae</i>	Ecuador, Morona-Santiago: Limón-Gualaceo rd.		KWJH	PENROS 2	
	<i>quinterae</i>	Ecuador, Zamora-Chinch.: Jimbura-S. Andrés rd.	PT	KWJH	PENROS 14	
	<i>quinterae</i>	Ecuador, Zamora-Chinch.: Jimbura-S. Andrés rd.	PT	TWP		
	<i>quinterae</i>	Ecuador, Zamora-Chinchipe: Valladolid	PT	MBLI		
	<i>quinterae</i>	Ecuador, Zamora-Chinchipe: Valladolid	PT	MBLI		
	<i>quinterae</i>	Ecuador, Loja: Cajanuma	PT	TWP	01/31.03.1999	12G
	<i>quinterae</i>	Peru, Cajamarca: Tabaconas	PT	TWP		
	<i>quinterae</i>	Peru, Cajamarca: Hacienda Udimá	PT	MUSM		
<i>golondrina</i>		Ecuador, Carchi: Santa Rosa, Res. Golondrinas	PT	KWJH	PENROS10	12H
<i>prattorum</i>		Peru: "W. Slopes of Andes"	PT	BMNH	6448	
<i>prattorum</i>		Peru: "W. Slopes of Andes"	PT	TWP	03/02.05.1999	12I
<i>prattorum</i>		Peru, Piura: Canchaque	PT	MUSM		
<i>trimaculata</i>		Ecuador, Zamora-Chinchipe: Loja-Zamora rd.		TWP	03/07.04.1999	13A
<i>trimaculata</i>		No data		BMNH	6447	
<i>undulata</i>	<i>undulata</i>	Ecuador, Loja: Guayquichuma	PT	TWP	09/07.04.1999	13B
	<i>undulata</i>	Ecuador, Pichincha: Río Las Palmeras	PT	KWJH	PENROS 7	
	<i>undulata</i>	Ecuador, Pichincha: Tandapi	PT	KWJH	PENROS 18	
	<i>undulata</i>	Ecuador, Cotopaxi: Pilaló	PT	TWP		
	<i>undulata</i>	Ecuador, Loja: Jimbura-San Andrés rd.	PT	TWP	03/25.01.1999	13C

APPENDIX 5 (Cont.)

Species	Subspecies	Locality	Type	Coll.	Dissection#	Fig.
<i>interrupta</i>	<i>milaena</i>	Peru, Cajamarca: Hacienda Udimá		MUSM		
<i>interrupta</i>		Ecuador, Azuay: Gualaceo-Chiguinda rd.		KWJH	PENROS 15	
<i>rufanalis</i>		Ecuador, Loja: Loja-Cuenca rd.		TWP	04/30.03.1999	13D
	<i>rufanalis</i>	Ecuador, Tungurahua: Río Machay	PT	KWJH	PENROS 1	
	<i>rufanalis</i>	Ecuador, Loja: Cajanuma	PT	TWP		
	<i>rufanalis</i>	Ecuador, Zamora-Chinchi: Qbda. San Ramón	PT	KWJH	PENROS 17	
	<i>rufanalis</i>	Ecuador, Zamora-Chinchi: Jimbura-S. Andrés rd.	PT	KWJH	PENROS 16	
	<i>rufanalis</i>	Ecuador, Zamora-Chinchi: "Zumba"	PT	TWP		
	<i>rufanalis</i>	Ecuador, Zamora-Chinchi: San Andrés	PT	TWP		
	<i>rufanalis</i>	Peru, Cajamarca: Tabaconas	PT	TWP	07/31.03.1999	13E
	<i>fernandina</i>	Ecuador, Azuay: Girón	PT	TWP	10/25.01.1999	13F
<i>ignilineata</i>	<i>ignilineata</i>	Ecuador, Loja: Jimbura-San Andrés rd.		KWJH	PENROS 20	14A
	<i>neglecta</i>	Ecuador, Cotopaxi: Pilaló		TWP	10/07.04.1999	14B
<i>seducta</i>		Peru, San Martín: Abiseo	PT	MUSM	01/22.06.2002	14C
<i>mycalesoides</i>		Venezuela, Barinas: Uribante		JFLC	74/1996	14D
<i>mycalesoides</i>		Venezuela, Táchira: Sierra de El Tamá		TWP		
<i>mycalesoides</i>		Venezuela, Miranda: Altos de Pipe		AFEN	NEILD 01	
<i>magnifica</i>		Peru, Amazonas: Falso Paquisha	PT	MUSM	07/27.04.2002	14E
<i>nevadensis</i>		Colombia: Sierra Nevada de Santa Marta		MA		
<i>nevadensis</i>		Colombia: Sierra Nevada de Santa Marta		BMNH	6444	14F
<i>levana</i>		Colombia, Cundinamarca: "Bogotá"		TWP		
<i>levana</i>		Colombia, Cundinamarca: "Env. Bogotá"		BMNH	6446	14G
<i>pervaga</i>		Venezuela, Táchira: Sierra de El Tamá	HT	MALUZ		14H

Phylogenetic, habitat, and behavioural aspects of possum behaviour in European lepidoptera

TIM G. SHREEVE

Oxford Brookes University, Department of Biological and Molecular Sciences, Headington, Oxford OX3 0BP, U.K.
tgshreeve@brookes.ac.uk

ROGER L.H. DENNIS

Oxford Brookes University, Department of Biological and Molecular Sciences, Headington, Oxford OX3 0BP, U.K.
NERC Centre for Ecology and Hydrology, Monks Wood, Abbots Ripton, Huntingdon, Cambridgeshire PE28 2LS, U.K.
rlhdennis@aol.com

ANDREW WAKEHAM-DAWSON

The International Commission on Zoological Nomenclature, c/o The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.
andrw@nhm.ac.uk

Abstract: We describe the behaviour of playing possum, or thanatosis, in mate rejection by non-receptive female butterflies of the Satyrinae of the Palearctic. In this behaviour females feign death with closed wings and release themselves from the substrate on which they are settled. This behaviour only occurs with extreme male persistence and is the final part of a mate-rejection behavioural sequence. We suggest that this behaviour may be relatively rare, possibly restricted to the tribes Elymini and Maniolini. There are potential associations with female mating frequency, male mate-locating mechanisms and the physical structure of habitats where attempted mating occurs. We suggest that the behaviour occurs in species where females occasionally mate more than once, where the predominant male mating strategy is a perching sit-and-wait tactic and the species occupy woodland structures. In such circumstances males have relatively few opportunities to mate, male-female encounter rates may be relatively infrequent and the physical structure of the habitat allows females that adopt possum mate-rejection to escape from males by dropping into vegetation. We encourage further observations on this behaviour to allow a thorough analysis of its frequency amongst species in order to allow a phylogenetic analysis.

Key words: predation, mate location, mate rejection, *Pararge*, *Lasiommata*, *Kirinia*, *Esperarge*, *Maniola*.

Playing possum (thanatosis: feigning death) in butterflies has been described for two very different circumstances. It was first described as a predator escape mechanism in *Gonepteryx rhamni* L. Pieridae (Dennis 1984) and *Inachis io* L. Nymphalidae (Dennis 1998). More recently, it has also been shown to have a role in mate refusal by females of *Pararge* and *Lasiommata* species (Satyrinae) (Shreeve 1985, Dennis 2003) and has been described for *Esperarge climene* (Satyrinae) (Wakeham-Dawson et al. 1999). As far as we are aware it has not been described in mate rejection for any other butterfly taxon apart from Satyrinae (nomenclature as in Karsholt & Razowski 1996). Here, we summarise the behavioural, morphological, habitat and phylogenetic attributes for these behaviours as

currently known; in doing so we focus attention on possum behaviour in mate rejection, the objective being to encourage further observations (Table 1).

In the Lepidoptera possum behaviour is a widespread secondary defence mechanism (Scoble 1992) and in the butterflies it has been recorded in species of Nymphalinae and Pieridae. On being caught by the wings, these species undergo thanatosis and effectively play dead. When released they will lie on their side inert for some time before taking flight (Dennis 1984, 1998). Species which adopt this behaviour tend to be long-lived and have relatively robust wings. As manipulation by birds can lead to wing damage, evidenced in tears and scored beak marks across wings of butterflies caught by birds (Collenette 1935, Bowers & Wiernasz 1979, Bengston 1981, Dennis et al. 1984), this would give butterflies with tougher wings an advantage over those with weaker structures. Butterflies described

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displaying possum behaviour in relation to predation typically hibernate as adults and have under-surfaces and wing shapes that characteristically mimic dead leaves. They spend much of the later summer feeding avidly on nectar and in such situations are particularly vulnerable to predation. *G. rhamni* are often so engrossed in feeding that they can be picked off the flower heads with ease (Dennis 1984). Experiments on possum behaviour indicate that the behaviour may be triggered more easily in autumn brood adults intent on accumulating resources for hibernation than in early summer broods actively engaged in mating. Although described thus far for *G. rhamni* and *I. io*, it is expected that this behaviour will extend to closely related species with similar life histories, morphology and behaviour (e.g., *Aglais urticae*).

Possum behaviour in mate rejection is the final stage of a behavioural sequence, with common elements to more normally widespread mate rejection behaviour. First, when harassed by a male attempting to copulate, a settled female may simply raise its abdomen to prevent copulation (e.g., *Pieris napi* L. Pieridae; *Plebejus argus*, L. Lycaenidae; Wilcockson 2002, Dennis, pers. observation). This may or may not involve wing fluttering as well. This behaviour, which may involve exposure of the genitalia with possible chemical signalling, is common to many butterfly taxa (Obara 1982, Obara 1984), but not all. In butterflies that adopt abdominal raising, there may be a second stage of mate-rejection in which a non-receptive female may attempt to prevent mating by completely closing its wings if the initial abdominal-raising proves unsuccessful. In butterflies that do not adopt abdominal raising, wing closing is usually the first stage to prevent mating by a persistent male. The genitalia of a closed wing female are then completely inaccessible to the courting male. Where possum behaviour differs from ordinary wing closing is in the subsequent stages. In possum-playing females the harassed female may lean over onto the substrate, effectively playing dead. Should the male persist then the female may then release its tarsal claws from the substrate on which it is settled and drop to lower vegetation or even the ground. In most instances when this occurs in *Pararge aegeria* L., and in the described behaviour of *Esperage climene* Esper, the male will lose the female and fly off (Shreeve 1985, Wakeham-Dawson et al. 1999). In other instances the male will pursue the female to the lower substrate or ground and persist in trying to enforce copulation before eventually giving up and flying off. This persistence may be long (max 65 sec. in *Pararge aegeria*, Shreeve 1985). In no instance has successful copulation of the apparently 'dead' female been recorded, either before or after

falling from a substrate. When a refusing female plays possum it will remain quiescent after the male leaves before resuming its activities (flight or basking). The two stages of orientation and dropping make possum behaviour unique. It appears to be part of females' mate-rejection repertoires when the total duration of male harassment is very long (Dennis 2003).

Recorded instances (Table 1) of females playing possum behaviour in response to attempted copulation by males is possibly restricted to the tribe Elymniini and one member of the tribe Maniolini, *Maniola jurtina* L. (Satyrinae, Maniolini). In the case of *M. jurtina*, this behaviour has been recorded in 4 instances out of 27 attempted courtships in dry Mediterranean scrub/woodland in Provence, France observed between 27 July and 11 August 1988 by one of us (TGS). As far as we are aware possum behaviour linked to mate-rejection has not been recorded in any higher taxa. Instances of similar, but not identical, behaviour are described in *Carterocephalus palaemon*, Hesperidae (Ravenscroft 1994: 1185) and females of other species will reject males by remaining quiescent during attempted courtships (e.g., *Leptidea sinapis* L. Dismorphiinae; Wiklund 1977). In the case of *C. palaemon* unreceptive females drop to the ground with closed wings when pursued by a flying male and the behaviour of *L. sinapis* is different from true possum behaviour in that unreceptive flying females detected by flying males sail to the vegetation and rest quiescent with closed wings. Restricting the analysis to the Satyrinae reveals that there are potential associations with female mating frequency, male mate-locating mechanisms and the physical structure of habitats where attempted mating occurs. Possum behaviour has not been recorded in those taxa where male access to already mated females is physically obstructed by a sphragis (mating plug) (e.g., *Hipparchia*, *Heteronympha*; Orr 2002). On the other hand, it has been recorded in those members of the Elymniini (*Pararge aegeria*, *P. xiphia* Fabricius, *P. xiphoides* Staudinger) and in *Maniola jurtina*, (Shreeve 1985, Dennis 2003, J. Tennent, personal communication) where females may occasionally mate more than once (*P. aegeria* 4–10% Wickman & Wiklund 1983, Shreeve 1985; *P. xiphia* 5% and *P. xiphoides* 8%, Shreeve unpublished; *M. jurtina* 4%, Maier, 1998). The mating frequency of *Esperage climene*, in which possum behaviour occurs, is not known. With one exception, female possum behaviour in mate-rejection has only been recorded in species in which the primary mechanism of mate-locating by males is perching and where perching occurs in predictable woodland structures, with males primarily settled on vegetation above the ground. Partial possum behaviour (in which females do not release

Table 1. The occurrence of possum behaviour in relation to habitat structural associations, mate locating methods, female mating frequencies and congruence of hostplants with mating areas in Palearctic butterfly taxa

Super-family	Family	Subfamily	Tribe/Species	Possum behaviour	Habitat structure	Primary male mate-locating mechanism	Female mating frequency	Egg-laying and mating location congruence	Hostplant location selectivity by laying females
Hesperioidea	Hesperiidae			-	Open short-medium length grassland and wasteland	Perching & patrolling	?	Variable	High
				-	Open grassland, scrub and scree	Perching or patrolling	Single	Variable	High
Papilionoidea	Papilionidae			-	Open grassland	Patrolling	Single	High	High
				-	Riparian, wet grassland, pioneer	Patrolling	Multiple	High	High
	Pieridae	Dismorphinae Pierinae		-	Open grassland	Patrolling	Multiple?	High	High
				AP	Woodland and scrub	Patrolling	Single	Low	High
Lycacnidae		Coliadinae	<i>Colias</i> spp.	-	All	Perching, lek or patrolling	?	Variable	High
			<i>Gonepteryx</i> spp.	-					
Nymphalidae		Libytheinae Heliconiinae Nymphalinae		?	Open woodland	?	?	?	High
				?					?
				AP	Open grassland, fen, scrub, woodland	Perching & patrolling	?	Variable	High
				-	Woodland	Perching	Single?	Low	High
		Limnitiinae Charaxinae Apaturinae Satyrinae		?	Woodland edge	Patrolling	?	Low	High
				-	Woodland	Perching	?	Low	High
			Elmniini	?	Woodland	Perching		High	High
			<i>Kirina roxelana</i>						
			<i>Esperage climeae</i>	+	Woodland	Perching		High	High
			<i>Pararge aegeria</i>	+	Woodland	Perching		High	High
			<i>Pixiphia</i>	+	Woodland	Perching	Multiple	High	High
			<i>Pixiphoides</i>	+	Woodland	Perching		High	High
			<i>Lasionomata megera</i>	-	Open grassland, pioneer, scrub	Perching	Multiple	High	High
				-					
			<i>L. petropitana</i>	-	Open grassland	Perching	?	High	High
			<i>L. paramegara</i>	-	Open grassland	Perching	?	High	High
			<i>L. macra</i>	-	Open grassland	Perching	?	High	High
				-					

Table 1 cont.

Super-family	Family	Subfamily	Tribe/Species	Possum behaviour	Habitat structure	Primary male mate-locating mechanism	Female mating frequency	Egg-laying and mating location congruence	Hostplant location selectivity by laying females
Danainae			<i>L.deidamia</i>	?	Open grassland	Perching	?	High	High
			<i>Lopinga achine</i>	+	Woodland	Perching	?	High	High
			<i>Ypthimini</i>	-	Open grassland/ pioneer structures/ scrub/bogs	Perching	?	Variable	?
			<i>Coenonymphini</i>	-					High
			<i>Manioliini</i>	-	Grassland/scrub	Patrolling	?	Low	Low
			<i>Pyronia</i> spp.	-	Open grassland	Patrolling	?	Low	Low
			<i>Aphantopus hyperantus</i>	-	Open grassland	Patrolling	Multiple	High	Low
			<i>Maniola</i> spp.	+ in <i>M.jurtina</i>					
			<i>Hyponomephele</i> spp.	?	Scree and scrub	Patrolling?	?	?	?
			<i>Erebini</i>	-	Grassland and open structures, bogs	Patrolling	?	Variable	Variable
			<i>Satyrini</i>	?	Open grassland	Patrolling	?	High	Low
			<i>Satyrus</i> spp.	?	Open grassland	Patrolling	?	Low	Low
			<i>Minois dryas</i>	-	Pioneers tructures/ open grassland	Perching	Single	Low	Low
			<i>Hipparchia</i> spp.	-					
			<i>Aethusena arethusena</i>	-	Pioneer structures/ open woodland	Perching	Single	Low	High
			<i>Brintesia</i> spp.	-	Scrub/woodland	Perching	Single	Low	High
			<i>Chazara</i> spp.	?	Pioneer structures	Perching	Single	Low	High
			<i>Pseudochazara</i> spp.	?	Pioneer structures	Perching	Single	Low	High
			<i>Oeneis</i> spp.	?	Pioneer structures	Perching	?	Low	High
				-	All except woodland	Patrolling	Multiple	Low	High

Nomenclature follows Karsholt & Razowski (1996)

+ recorded as occurring, - recorded as not occurring, ? no data, AP predator escape mechanism

Multiple female mating frequency = known instances of females mating more than once

from the substrates they are on) occurs within the *Laesiommata* genus, but in all instances occurrences have taken place on bare ground substrates (T.G. Shreeve, personal observation). Recorded instances of possum behaviour by females of *Maniola jurtina* have been in woodland structures in southern Europe where summer aestivation occurs. With the exception of *Maniola jurtina*, females that adopt possum behaviour are also highly selective of the locations in which they lay eggs, even if plant species on which larvae feed are themselves widespread.

Whilst information on the details of mate rejection by females of the majority of species is extremely scant, the provisional analysis that we supply here is itself revealing of a possible phylogenetic component with links to the overall behaviours of both sexes and the physical structure of the habitats in which species occur. The occurrence of female possum behaviour as a mate rejection behaviour can be explained by a common set of characteristics; females potentially mating more than once, occupation of specific woodland structures, the occurrence of perching within the mate locating repertoire and selectivity by females for specific egg-laying locations. A common element of female possum behaviour is that it only occurs after other mate-rejection postures, such as abdominal raising, wing fluttering and wing closing, have failed to deter the male. It is also potentially time consuming for both the male and even more so for the female, which will tend to remain quiescent after the courting male has left.

If females easily and unequivocally communicate their non-receptivity then it is pointless for any male to spend time attempting to court a non-receptive female. In such circumstances it is unlikely that female possum behaviour will be employed or even develop. Thus the behaviour is absent where there is the clear signal of a sphragis in single mating females (e.g., *Hipparchia*, Satyrinae). It is also absent where there is multiple mating, but unreceptive females are plugged with a sphragis and males have limited resources to make plugs (e.g. *Heteronympha* species) or where effective chemical signalling associated with abdominal raising occurs in potentially multiple mating females (e.g. *Pieris* spp.; Pieridae, Obara & Hidaka 1964). It is also apparently absent in species in which receptive females have specific behaviours to advertise their receptiveness to males such as the jumping flights of virgin *Aphantopus hyperantus* L. (Maniolini) (Wiklund 1982). Efficient communication of receptiveness is advantageous to females since they will not spend time harassed by males. When males are given an unambiguous early cue of non-receptivity then they are unlikely to harass, so more complex rejection

behaviours may not be developed.

In species in which female possum behaviour occurs the primary male mate locating mechanism is perching. Perching males sit and wait for females and their persistence with individual females may be high to try and enforce copulation with relatively scarce females. If mated females fly into areas where perching males detect them they do so because they are searching for other resources (e.g. egg-laying sites, nectar sources). In the case of *Pararge* species, females are highly selective of egg-laying sites (e.g. Shreeve 1985, 1986, Shreeve & Smith 1992) and possum behaviour may be the only sure mechanism of deterring a courting male if the female is in a suitable egg-laying location. Time spent playing possum may be less than time spent searching for alternative resources elsewhere. In the case of *Pararge aegeria*, the maximum recorded time playing possum (65 seconds) is within the range of times spent on searching flight between egg-laying locations (Shreeve 1985).

Female possum behaviour may be absent in strictly patrolling species. We suggest that it has not developed in this circumstance because in such species females are readily apparent to males by colouration (Dennis & Shreeve 1988) or are abundant. Thus it may be unproductive for males to persist with an unreceptive female since others will be readily detected or encountered. Similar arguments apply to lekking species (e.g. some Theclinae); the majority of females entering a lek will be receptive.

Although we have limited data, it is possible that female possum behaviour may be restricted to species that use a specific set of woodland structures, though not universally so. For example, it has not been recorded for species that locate mates primarily within the woodland canopy (e.g. *Argynnis* species, Nymphalidae; *Neozephyrus* species, Lycaenidae) or on the ground layer of woodland (e.g. *Arethusena* species, Nymphalidae).. One key characteristic of those species that use this form of possum behaviour is the resemblance of the wing underside to dry leaves, which are predictable components of the ground layer. As examples, *Argynnis* and *Neozephyrus* species may be highly conspicuous to conspecifics and predators when on the ground layer and adoption of possum behaviour may increase predation risk. The absence of possum behaviour from multiple mating species of grassland and more open structures such as rock slopes may also be related to wing and substrate colouration, with the latter tending to be more variable than in woodland. In such circumstances any individual playing possum may render itself conspicuous and vulnerable to predation. We suggest that contrast of underside wing colouration with background is itself a constraint on

the development of possum behaviour.

Whilst the information on this behaviour is rather limited there are indications that it may also have a phylogenetic component. The adoption of possum behaviour in mate-rejection appears restricted to one or perhaps two tribes of the Satyrini. It may also be a derived trait associated with their adoption of woodland structures from ancestral open grassland structures (Dennis & Shreeve 1988). Evidence for the possible restriction of possum behaviour to the tribe Elymiini within the Satyrinae comes from its apparent absence from the behavioural repertoire of *Lethe diana*, which also occupies woodland structures (Ide 2002). Where possum behaviour occurs in other taxa (e.g. Nymphalinae and Pieridae), as indicated above, it is a primary response to predator attack and the species which adopt such a behaviour are long lived and have relatively thicker and more robust wings than the Satyrini (Table 1). We suggest that a more detailed examination of possum behaviour would reveal much about the interrelationship of behaviour with habitat structural predictability and costs and benefits of individual behavioural traits. In particular, information on the extent of its occurrence is required for a full analysis and a proper test of hypotheses to account for its occurrence. We would welcome observations.

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NOTES

Observations on the shelter building behavior of some Asian skipper larvae (Lepidoptera: Hesperiidae)

INTRODUCTION

The larvae of many lepidopteran families modify their immediate environment by cutting, folding, rolling, and/or silking portions of their foodplant into a shelter (DeVries 1987, 1997, Scoble 1992, Stehr 1987). While only a few species have been investigated in detail, the possible functions of these structural retreats include reduced predation (Eubanks et al. 1997, Jones et al. 2002), prevention of dislodgment (Loeffler 1996), and creation of a more favorable microclimate (Henson 1958). Among the most prolific groups of shelter building larvae are the Hesperiidae, most of whom, with only a few exceptions (eg. Moss 1949, Scudder 1889), have been reported to construct shelters. A recent review of hesperiid larval shelters found there to be 10 basic shelter types constructed by skipper larvae, and pointed to the possible importance of shelter form for phylogenetic analysis (Greeney & Jones 2003). Here we use the classification and terminology proposed by Greeney & Jones (2003) to describe the shelters built by 4 species of hesperiids from China and the Philippines. Only shelters built in nature were considered.

SPECIES ACCOUNTS

Capila translucida (Leech 1893). Larvae were reared on *Cinnamomum camphora* (Lauraceae) in Ru Yang, Peoples Republic of China. Larvae of all instars rest upside down inside their shelters, attaching their crochets to a pad of resting silk laid down on the inside of the shelter lid. No frass accumulated within the shelters, and larvae of all instars forcibly eject frass from the anus. First instars were found to build Group II Type 5, center-cut folds. These are built by cutting into the middle of the leaf, away from the margin. The cut is nearly circular, with the proximal and distal ends converging outwards from the circular portion to give the cut an overall paddle shape. This round flap is then folded over at the narrow shelter stem to create a man-hole-like retreat (Fig. 1a). Later instars build Group III Type 10, two-cut stemmed folds. These are roundly triangular portions of the leaf cut from the margin using two cuts. The cuts curve towards each other near their distal ends and finally run parallel

to create a narrow shelter stem. This narrow stem is heavily silked to pull the flap over to meet the leaf surface (Fig. 1b). Often a minor cut is made on the edge of the shelter lid (Fig. 1h). Opposite sides of this small cut are then silked together to pinch the lid into slightly peaked or tented form. This modification is also occasionally accomplished without a cut, by simply laying silk along the lid margin to pinch it upwards into a peak. These modifications presumably give the larvae more room to maneuver inside the shelter. Final instars may build Type 10 shelters or may construct Group I Type 4, two-leaf shelters. Type 4 shelters are made by silking two leaves together to create a shallow pocket. The first instar shelter built by *C. translucida* is very similar to that recently reported for first instars of the pyrgine, *Noctuana haematospila* (C. Felder & R. Felder 1867), in Ecuador (Greeney & Warren 2004). The ontogenetic changes in shelter type, however, are quite different. For a description of the egg, larvae, and pupa of *C. translucida* see Young & Chen (1999).

Tagiades litigiosus litigiosus (Möschler, 1878). Larvae were reared on *Dioscorea fordii* (Dioscoreaceae) in Kau Tam Tso, Wu Kau Tan, and Tai Po, Hong Kong. Larvae of all instars rested upside down on the shelter lid, and kept their shelters clean by ejecting frass away from the shelter. First through fourth instars built Group III Type 9, two-cut unstemmed folds. These were built by making two cuts originating at the leaf margin which converged slightly towards their distal ends to create a broad shelter stem over which the resulting flap was folded onto the leaf surface. This created a broadly folded, roundly rectangular or square shelter (Fig. 1c). Heavy resting silk on the inside of the shelter lid caused the shelter to bowl slightly, giving the larvae more room inside their retreat. Often the bridge (portion where the stem is folded) was scored along the inside by cutting only through the leaf epidermis to weaken the folding point. Final instars either constructed a larger version of the Type 9 shelters described above, or made Group I Type 4, two-leaf shelters by silking two adjacent leaves into a shallow pocket. The ontogenetic changes in shelter type, as well as the individual shelters used by each instar were very similar to the shelters described for larvae of the pyrgine *Eantis thraso* (Hübner, 1807) in

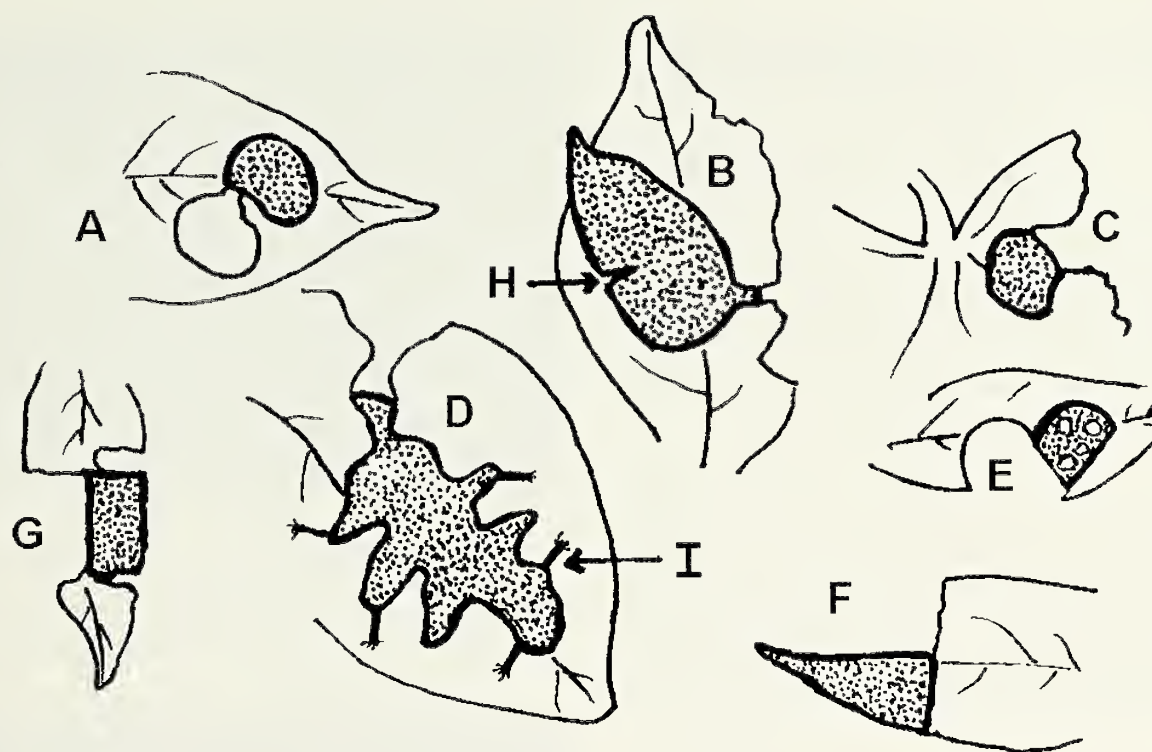


Fig. 1. Shelters built by larvae of Asian skippers: Shelters not drawn to scale, stippled areas represent the area hiding the larvae from view. A) First instar of *Capila translucida* on *Cinnamomum camphora*, Ru Yang, Peoples Republic of China. B) Fourth instar of *C. translucida* on *C. camphora*, Ru Yang, Peoples Republic of China. C) First instar of *Tagiades litigiosus* on *Dioscorea fordii*, Hong Kong. D) Final instar of *Coladenia agnioides* on *Eriobotrya fragrans*, Ru Yang, Peoples Republic of China. E) First instar of *Bibasis sena palawana* on *Hiptage bengalensis*, Los Baños, Philippines. F) Final instar of *B. sena palawana* on *H. bengalensis*, Los Baños, Philippines. G) Final instar of *B. sena palawana* on *H. bengalensis*, Los Baños, Philippines showing isolation of shelter by feeding damage. H) Secondary cut to allow tenting of shelter lid by fourth instar of *C. translucida*. I) Externally visible tying silk, securing shelter lid of final instar of *C. agnioides*.

Ecuador (Greeney & Warren 2003).

Coladenia agnioides (Elwes & Edwards, 1897). Larvae were reared on *Eriobotrya fragrans* (Rosaceae) in Ru Yang, Peoples Republic of China. Frass was never observed to accumulate inside the larval shelters. Final instar larvae built Group III Type 10, two-cut stemmed folds. The two major cuts, initiated from the leaf margin, angled towards each other then ran parallel for some distance to create a narrow stem. At their distal ends, however, the cuts separated slightly to create a bridge which was broader than the stem. Larvae scored the inside of the bridge, presumably to facilitate folding. After constructing this long-stemmed, triangular shelter, larval feeding damage created large channels cut in from the margins of the shelter lid, giving the lid margins a jagged appearance. The final product, therefore, took on a form similar to a Christmas tree (Fig. 1d). Strong lines of tying silk attached the rim of the shelter lid to the surrounding leaf (Fig. 1i). A heavy pad of resting silk, laid in a

roughly circular pattern on the inner surface of the shelter lid, caused the lid to bowl slightly. The channels, by weakening the structural integrity of the lid, likely aided in this process.

Bibasis sena palawana (Staudinger, 1889). Larvae were reared on *Hiptage bengalensis* (Malphigiaceae) at Mount Mikiling, Los Baños, Philippines. Early instars built Group III Type 9, two-cut unstemmed folds. One primary cut, beginning at the leaf margin, was long and arcing, curving back towards the leaf margin. The second primary cut was much shorter, approaching the distal end of the larger cut directly from the leaf margin, but leaving a broad shelter bridge with no stem. The resulting flap was then folded to the leaf surface. This created a distinctly shaped shelter lid, rounded on one side, and straight along the portions consisting of the leaf margin and along the shelter bridge (Fig. 1e). The lid was not bowled or tented in any way and remained tightly appressed to the leaf surface. This shelter was then modified with several

perforations in the shelter lid, created by larval feeding damage. Later instars built a Group II Type 6, one-cut fold by making a single large cut near the distal portion of the leaf. This cut extended from the leaf margin, directly to the midvein. This side of the cut was then drawn together with the opposite leaf margin creating a large, flattened pocket (Fig. 1f). Heavy feeding damage around the area where the larvae rested often resulted in this portion of the shelter being nearly isolated from the surrounding leaf (Fig. 1g). If the original shelter had not been seen, the final product could easily be mistaken for a Group II, Type 9, two-cut unstemmed fold.

While there has been too little published concerning the details of larval shelter construction to make comparisons between and among taxa, these data provide evidence that the classification system provided by Greeney & Jones (2003) is a useful tool in a variety of geographic regions. We hope this note encourages others to publish similar details so that such architectural features may be used in the development and testing of phylogenetic hypothesis.

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HAROLD F. GREENEY, Yanayacu Biological Station & Center for Creative Studies, Cosanga, Ecuador c/o 721 Foch y Amazonas, Quito, Ecuador.
E-mail: revmmoss@yahoo.com

JAMES J. YOUNG, 4950 Connaught Drive, Vancouver, B.C. Canada V6M 3E9

An interspecific mating attempt between a male *Siproeta epaphus* Latreille and a female *Anartia amathea* Linnaeus (Lepidoptera: Nymphalidae).

Interspecific mating attempts between lepidopterans are not uncommon (eg. Davies *et al.* 1997, Deering & Scribner 2002). Here we report an attempted copulation between two nymphalid species, *Siproeta epaphus* (Latreille 1819) and *Anartia amathea* (Linn. 1758) in western Ecuador. Observations were made

at the Sachatamia Lodge (0.01. 35 S 78.45.34 W) near the town of Mindo, Pichincha Province, at 1700 m elevation.

On 6 July 2004, at approximately 11:30 am, a male *S. epaphus* was seen and photographed in copula with a female *A. amathea* (Figure 1). Upon closer examina-



Fig. 1. Male *Siproeta epaphus* in copula with a female *Anartia amathea* at 11:30 am, northwestern Ecuador. Photo by H. F. Greeney.



Fig. 2. Close up of coupling of a male *Siproeta epaphus* and a female *Anartia amathea* in northwestern Ecuador. Inset shows resulting damage to female abdomen. Photo by H. F. Greeney.

tion, it could be seen that, rather than being joined at the genitalia, the male's claspers were attached to the side of the female's abdomen around segment 7 or 8. The exoskeleton of the female was ruptured, and fluids and internal organs were pushing out around the male's claspers (Figure 2). Damage was so severe, it is likely that the female had lost her reproductive capacity, and we doubt sperm transfer was possible. Both individuals were collected and deposited in the Museo Ecuatoriano de Ciencias Naturales in Quito.

The close relationship between *Anartia* and *Siproeta* is well supported (Freitas & Brown 2004, Wahlberg *et al.* 2005), and both genera feed on plants in the family Acanthaceae (DeVries 1987). As plant-derived compounds may be used to derive intraspecific com-

munication pheromones (eg. Conner *et al.* 1981, Schultz *et al.* 1993), similarities in sex attractants may have resulted in the observed mistake.

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HAROLD F. GREENEY, Yanayacu Biological Station & Center for Creative Studies, Cosanga, Ecuador c/o 721 Foch y Amazonas, Quito, Ecuador. E-mail: revmmoss@yahoo.com

WANDA DAMERON, 23424 Jonathan Street, Los Angeles, California 91304, USA

HANK BRODKIN, 3050 East Carr Canyon Rd, Hereford, Arizona, 85615, USA

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